“ Plants do what they want ”

**Kathleen B. Pigg**

“ A quiet body of fresh water … ”

**Georgia L. Hoffman**

“ Plants are smaller in the fossil record ”

**Ruth A. Stockey**

University of Alberta

# The importance of paleobotanical whole plant reconstructions: morphology and anatomy of Lythraceae and Lauraceae from the Princeton Chert.

by

Stefan Allan Little ©

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# Abstract

This dissertation presents new data on two fossil angiosperm species from the Middle Eocene Princeton Chert, British Columbia, Canada: *Decodon allenbyensis* Cevallo-Ferriz et Stockey (Lythraceae, loosestrife family), and *Similkameena borealis* gen. et sp. nov., (Lauraceae, laurel family). Several criteria are used to reconstruct plants: 1) close association of organs in same chert blocks, 2) consistent co-occurrence of organs in a chert layer, 3) anatomical comparisons to extant and fossil taxa, 4) anatomical characters shared by isolated organs, 5) developmental sequences that connect isolated organs at different stages of maturity, and 6) attachments of plant organs.

*Decodon allenbyensis*, originally described based only on fruits and seeds, is reinvestigated on the basis of vegetative remains. Anatomy of both stems and roots of the extant, monotypic *Decodon verticillatus* (L.) Ell. is also described and compared to the fossil axes. A further developmental study on roots of *D. allenbyensis* indicates a pattern of anatomical changes that is distinct from that seen in members of the sister family Onagraceae (evening primrose family). In addition, this developmental study also reveals an attachment of roots to large axes bearing a novel type of aquatic bark. This level of developmental information is unknown in other extant or fossil Lythraceae. Finally, a comparative study on leaves of extant Lythraceae *sensu lato* reveals a combination of anatomical characters diagnostic for *Duabanga grandiflora* Roxburgh ex DC Walpers (Subfamily Duabangoideae) that match those in fossil leaves associated with the axes of *Decodon*. The mutual abundance and association of *Decodon* axes and *Duabanga*-like leaves in the chert produces the hypothesis that these leaves are those of *Decodon allenbyensis*.

*Similkameena borealis* is represented by inflorescence axes that reveal a unique combination of inflorescence architecture and floral organization. My investigations show a developmental sequence from young flowers to mature fruits. This sequence allows for the amplification of the concept of *Similkameena* and is the first study of fruit development in fossil Lauraceae. Moreover, the fruit characters contribute to the distinctiveness of the taxon, and show that different developmental stages of the same species, preserved in the fossil record, may be dubiously assigned to separate taxa.

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To those who may find this useful or interesting

# TABLE OF CONTENTS

**CHAPTER 1. Introduction.**

LYTHRACEAE 5
LAURACEAE 6
LITERATURE CITED 9

**CHAPTER 2. Vegetative growth of *Decodon allenbyensis* (Lythraceae) with anatomical comparisons to *Decodon verticillatus*.**

INTRODUCTION 24
MATERIAL AND METHODS 26
RESULTS 28
  Roots 28
    *Decodon allenbyensis* 28
      Fossil root wood description. 29
    *Decodon verticillatus* 30
      Extant *D. verticillatus* root wood description 30
  Phellem 31
    *Decodon allenbyensis* 31
    *Decodon verticillatus* 32
  Stems 32
    *Decodon allenbyensis* 32
      Fossil stem wood description 33
    *Decodon verticillatus* 34
      Extant stem wood description 35
  Habit 36
    *Decodon allenbyensis* 36
DISCUSSION 36
LITERATURE CITED 49

**CHAPTER 3. Morphogenesis of specialized peridermal tissues in *Decodon allenbyensis*.**

INTRODUCTION 73
MATERIALS AND METHODS 74
RESULTS 75
  Primary growth 75
  Transition to secondary growth 76
  Secondary growth 76
    Xylem 76
    Phloem 77
    Phellem 77
    Rhytidome 77
DISCUSSION 78
LITERATURE CITED 85

**CHAPTER 4. *Duabanga*-like leaves and comparative leaf histology of Lythraceae *sensu lato*.**

INTRODUCTION 103
MATERIALS AND METHODS 105
RESULTS 106
  Fossil leaves 106
  Leaves of *Decodon verticillatus* (L.) Ell. 107
  Leaves of other extant Lythraceae 108
DISCUSSION 117
LITERATURE CITED 124
APPENDIX: Index of specimens shown in the plates. 143

**CHAPTER 5.** ***Similkameena borealis*** **gen. et sp. nov. (Lauraceae), flowers and inflorescences.**
- INTRODUCTION 145
- MATERIALS AND METHODS 147
- SYSTEMATICS 148
  - Generic diagnosis 149
  - Specific diagnosis 149
  - Description 150
- DISCUSSION 153
  - Comparisons to fossil Lauraceae 155
    - Fossil taxa: three-dimensionally/anatomically preserved 156
    - Fossil taxa: compression/impressions 162
  - Comparisons to extant Lauraceae 164
  - Conclusions 168
- LITERATURE CITED 170

**CHAPTER 6.** **Fruit development and anatomy of** ***Similkameena borealis*** **(Lauraceae).**
- INTRODUCTION 195
- MATERIALS AND METHODS 197
- SYSTEMATICS 199
  - Amplified generic diagnosis 199
  - Amplified specific diagnosis 199
  - Description 200
    - General sequence of development 200
    - Flowers and early fruit development 201
    - Immature fruit stage 202
    - Late immature fruit stage 202
    - Mature fruit stage 204
- DISCUSSION 205
  - Comparisons to fossil Lauraceae 208
  - Comparisons to extant Lauraceae 212
- LITERATURE CITED 216

**CHAPTER 7.** **Conclusions.**
- CHAPTER 2 241
- CHAPTER 3 242
- CHAPTER 4 244
- CHAPTER 5 245
- CHAPTER 6 246
- CONCLUDING REMARKS 248
- LITERATURE CITED 251

## LIST OF TABLES

CHAPTER 4

**Table 4.1.** Selected anatomical features for leaves of Lythraceae. 142

CHAPTER 5

**Table 5.1.** Inflorescence and flower characters of the extant genera of Lauraceae. 191

CHAPTER 6

**Table 6.1.** Characters of tepals on mature fruits of extant genera in Lauraceae. 238

**Table 6.2.** Cupule characters on mature fruits of extant genera in Lauraceae. 239

# LIST OF FIGURES

## CHAPTER 1

Geographical map showing location of the Princeton Chert. 22
Stratigraphic column of the Paleogene indicating age of the Princeton Chert 23

## CHAPTER 2

**Fig. 2.1** *Decodon allenbyensis* rooting systems. 58
**Fig. 2.2** *Decodon allenbyensis* and *Decodon verticillatus* stems and roots. 60
**Fig. 2.3** Fossil *Decodon allenbyensis* roots. 62
**Fig. 2.4** *Decodon allenbyensis* (fossil) and *Decodon verticillatus* (extant) roots under SEM. 64
**Fig. 2.5** *Decodon verticillatus* root wood anatomy. 66
**Fig. 2.6** Phellem of fossil and extant *Decodon*. 68
**Fig. 2.7** Extant and fossil *Decodon* stems. 70
**Fig. 2.8** *Decodon verticillatus* stem wood under SEM. 72

## CHAPTER 3

**Fig. 3.1** Roots of *Decodon allenbyensis* prior to, and shortly after secondary tissue production. 90
**Fig. 3.2** Roots of *Decodon allenbyensis* 92
**Fig. 3.3** Roots of *Decodon allenbyensis* 94
**Fig. 3.4** Phellem in roots of *Decodon allenbyensis* 96
**Fig. 3.5** Phloem and rhytidome of *Decodon allenbyensis* 98
**Fig. 3.6** Diagram representing *Ludwigia*-type and *Decodon*-type morphogenetic stages in aquatic roots 100
**Fig. 3.7** Diagram representing a new complex aquatic rhytidome 102

## CHAPTER 4

**Figs. 4.1–4.10** Transverse sections of fossil lythraceous leaves. 131
**Figs. 4.11–4.14** Scanning electron microscopy of *Decodon verticillatus* leaves. 133
**Figs. 4.15–4.22** Transverse sections of leaves of Lythraceae (Lythroideae and Duabangoideae). 135
**Figs. 4.23–4.27** Transverse sections of leaves of Lythraceae (Lythroideae). 137
**Figs. 4.28–4.30** Transverse sections of leaves of Lythraceae (Lythroideae). 139
**Figs. 4.31–4.34** Transverse sections of leaves of Lythraceae (Punicoideae and Sonneratioideae). 141

## CHAPTER 5

**Fig. 5.1** *Similkameena borealis* gen. et sp. nov. longitudinal sections of inflorescences. 179
**Fig. 5.2** *Similkameena borealis* gen. et sp. nov., oblique sections through inflorescences (A, B), and transverse sections through flowers (C, D). 181
**Fig. 5.3** *Similkameena borealis* gen. et sp. nov., longitudinal sections through flowers and stamens. 183
**Fig. 5.4** *Similkameena borealis* gen. et sp. nov., flower structure and details of inflorescence tissues. 185
**Fig. 5.5** *Similkameena borealis* gen. et sp. nov., floral diagrams. 187
**Fig. 5.6** *Similkameena borealis* gen. et sp. nov., inflorescence diagram. 189

## CHAPTER 6

**Fig. 6.1** Flowers and early fruit development. 227
**Fig. 6.2** Early fruit development. 229
**Fig. 6.3** Immature fruit stage. 231
**Fig. 6.4** Late immature fruit stage. 233
**Fig. 6.5** Late immature fruit stage continued. 235
**Fig. 6.6** Mature fruit stage. 237

# CHAPTER 1: Introduction

Paleobotanical investigations in the last 180 years have developed several approaches, influenced by preservation type. Early works were often large studies that attempted to account for all remains collected in a series of localities in a geographical region (e.g., Heer 1856; Berry 1914). These compression/impression "floras" were published as a large volume, or series of volumes. Such works are clearly important early contributions to the understanding of past diversity of plants over geological time, as well as early estimates of paleoecology and paleoclimate. However, these same works often suffered from a pressure to place plant fossils in extant genera (Dilcher 2000).

More recently, paleobotanical research has focused more on the systematics and evolutionary ramifications of plant fossils, especially with the introduction of cladistic analysis into the field (Crane 1985a, 1985b; Crepet et al. 2004). As a result, in order to perform a cladistic analysis, paleobotanists now require a series of parallel characters scored for each fossil taxon (Bateman et al. 1992; Nixon et al. 1994). As a result, it is well established that the inclusion of fossils in phylogenetic analyses can alter tree topologies based only on extant taxa (Gauthier et al 1988, Donoghue et al. 1989; Crane et al. 2004). Furthermore, fossils are becoming widely used in evolutionary rate calibrations and time estimates in phylogenetic analysis (Hulsenbeck 1994; Pryer et al. 2004; Sanderson et al. 2004).

Less common is an approach where fossils are used as a foundation on which to base phylogenetic hypotheses (DiMichele 1985; Rothwell and Serbet 1994; Rothwell 1999; Hernandez-Castillo 2006; Hilton and Bateman 2006). There are various opinions as to why fossils may be overlooked. My opinion is that there is a paucity of systematists who are comfortable with the breadth of fossil data, that there are too few paleobotanists in relation to the number of plant systematists, and that molecular data are becoming easy to accumulate and are widely considered to produce the most well supported phylogenies. Using only extant taxa to produce an evolutionary history of a group can yield misleading or inaccurate phylogenies, especially where there are homoplasious characters, and/or a high degree of extinction in a previously diverse group (Hulsenbeck 1991). The use of fossils as a main source of data for cladistic analysis is rare, but promises to be a powerful tool in studies of evolution and systematics (Hilton and Bateman 2006).

The difficulty in using data based on plant fossils for cladistic analysis is that fossilized plants are not complete upon first examination. Often, parts are found disarticulated from the parent plant, and may have been transported and sorted prior to preservation (Stewart and Rothwell 1993). The incompleteness of the fossil record, and the incompleteness of the plants preserved, is an often used argument against the use of fossils for understanding evolutionary history. However, whole plant reconstructions have been produced, representing fossil organisms with vegetative and reproductive characters known (e.g., Crane and Stockey 1985; Bateman et al. 1992; Manchester et al. 1998; Hernandez-Castillo et al. 2001; Stockey et al. 2001). This is often the result of detailed investigations at a locality, or series of localities, involving large numbers of specimens, correlation of organs at different localities (Crane and Stockey 1985, Manchester et al. 1998, Stockey et al. 2001), and the identification of rare attachments (Kvaček and Sakala 1999, Manchester et al.1989).

Fossil plants that are understood in detail have been shown to be the most useful for cladistic analyses, compared to those with fewer known characters (Hilton 2004). However, there is evidence that fossils, even only partially known, can improve resolution in cladistic analyses. In general, phylogenetic trees are considered more reliable when more characters are known for the taxa in an analysis, because homoplasious characters are less likely to mislead the results of the analysis (Felsenstein 2004). In addition, a fossil plant, with both vegetative and reproductive organs known, often shows a mosaic of characters not seen among the extant taxa to which it is related. This “mosaicism” has been touted as a key feature of fossils that is useful in both cladistic analyses, and tests of non-fossil based phylogenies (Crepet et al. 2004). Thus, it is important that at least some paleobotanical endeavors focus on producing as complete a plant concept as possible in order to contribute useful data to produce and test evolutionary hypotheses.

The Middle Eocene Princeton Chert locality (Fig 1.1, 1.2) is a well-studied site that has yielded numerous descriptions of permineralized plants (Pigg and Stockey 1996; Stockey 2001). Many of the plants described from the Princeton Chert are based on fruits, seeds, or vegetative organs such as shoots. Previous studies have established that the Princeton Chert preserves a wetland biota with several plants found *in situ*, rooted and in growth position (Cevallos-Ferriz et al. 1991). Conifers, ferns, fungi, and numerous angiosperms are known, as well as remains of soft-shelled turtles, mammals and fish from the overlying shales (Pigg and Stockey 1996). In addition, palynological work has been done on the coals that interbed with the chert layers (Boneham 1968), and ongoing palynological investigations are in progress, analyzing palynomorphs from the chert layers (R. Zetter, Univ. Vienna, in progress). The often *in situ* or parauthocthonous remains in the chert and their excellent anatomical preservation provide valuable opportunities to reconstruct plants more fully (e.g., *Eorhiza/Princetonia*: Robison and Person 1973; Pigg and Stockey 1991; Stockey and Pigg 1994; *Metasequoia milleri*: Basinger 1976, 1981, 1984; Basinger and Rothwell 1977; Rothwell and Basinger 1979).

Whole plants in the fossil record, with both vegetative and reproductive organs known, are rare due to the shedding of organs, and transport with sorting prior to preservation (Gastaldo 2001). Several criteria are used in studying the Princeton Chert, in order to connect the various organs, here called "reconstruction criteria": 1) close association of organs in the same chert blocks, 2) consistent co-occurrence of organs in a chert layer, 3) anatomical comparisons to extant and fossil taxa, 4) anatomical characters shared by isolated organs 5) developmental sequences that connect isolated organs at different stages of maturity, and 6) attachments of plant organs. Historically, the attachments of plant organs have often been used to amplify taxon concepts from a fossil locality. These data are ideal, especially at localities where the predominant preservation is by compression/impression. However, using several, or all, of the criteria above can produce compelling arguments for an expanded or whole-plant concept for fossils at the Princeton site.

The series of chapters in this dissertation are the result of efforts to employ the reconstruction criteria to plant remains at the Princeton Chert. Chapters 2-4 are studies of lythraceous remains, and chapters 5-6 are studies of lauraceous remains.

## LYTHRACEAE

Lythraceae (Order Myrtales), includes ca. 31 genera and 600 species occurring worldwide (Graham et al. 1993; Graham et al. 2005). Koehne (1903) circumscribed the family with 28 genera, all sharing the following characters: opposite, entire leaves; a persistent, perigynous, campanulate to tubular floral tube with crinkled petals inserted at the rim; two whorls of stamens inserted deep in the tube; and a many-seeded capsular fruit. It is widely accepted that the family should now also include the genera: *Trapa* L. (formerly Trapaceae), *Punica* L. (formerly Punicaceae), as well as *Duabanga* Buchanan-Hamilton and *Sonneratia* L.f. (formerly Sonneratiaceae) (Graham et al. 1998). Plants are generally terrestrial, but many are semiaquatic to aquatic (Schrenk 1889; Graham 1964; Sculthorpe 1967; Graham et al. 1993). This expansion of the family is the result of several studies, especially more recent phylogentic analyses using morphological data (Johnson and Briggs 1984; Graham et al. 1993), as well as molecular characters (Conti et al. 1996, 1997; Shi et al. 2000; Huang and Shi 2002; Graham et al. 2005).

The oldest fossil records of Lythraceae are seeds from the Campanian (Cretaceous) of Mexico (Rodríguez-de la Rosa et al. 1998) and later from the Paleocene of southern England (Reid and Chandler 1933; Chandler 1961). Fossils of Lythraceae include fruits, seeds, leaves, and pollen (Graham and Graham 1971; Muller 1981; Tiffney 1981; Friis 1985). In particular, the genus *Decodon* J. F. Gmelin, is known mainly based on seeds and fruits (Cevallos-Ferriz and Stockey 1988; Matsumoto et al. 1997; Bertram 1998; Kvaček and Sakala 1999), but compression/impression leaf fossils have been reported from from North America (Wolfe and Tanai 1980; Wehr and Hopkins 1994;

Stockey and Wehr 1996) and western Europe (Kvaček and Sakala 1999). Thus far, the most complete fossil *Decodon* species, described by Kvaček and Sakala (1999), has fruits with seeds attached to a leaf-bearing shoot. Cuticle data is known for the leaves of this plant, but no cellular anatomy is preserved. Part of this dissertation documents both anatomical and developmental details for the fossil *Decodon allenbyensis*.

Cevallos-Ferriz and Stockey (1988) first described the permineralized fruits and seeds of *Decodon allenbyensis* from the Princeton Chert. Chapters 2-4 investigate associated remains that are consistently found with the fruits and seeds of *D. allenbyensis*. Investigations of root and stem anatomy for the extant, monotypic *D. verticillatus* (L.) Ell. are used to expand the data already known for this species. These data are used for comparison to the fossil roots and stems at Princeton. In addition, attachments are shown for the fossil stems and roots. A developmental series illustrates the morphogenesis of the aquatic roots and is contrasted with that of members of the sister family Onagraceae, reported to have similar aquatic roots (Schenk 1889; Ellmore 1981). This developmental sequence also provides evidence for a novel type of aquatic rhytidome-like periderm in the most mature axes. A comparative study on leaves of Lythraceae, undertaken to determine the identity of the abundant leaves associated with the seeds and fruits of *D. allenbyensis*, indicates that the plant combines characters found in species of different genera.

## LAURACEAE

Chapters 5 and 6 investigate remains considered to be those of Lauraceae in preliminary investigations (Sun and Stockey 1991; Penner 1996). A large eumagnoliid family (*sensu* Soltis et al. 2000), Lauraceae contains 2500–3500 species, distributed pantropically (Rohwer 1993). Species are all woody shrubs or trees, with the exception of *Cassytha* L., which is a parasitic twiner (Weber 1981). Members of the family are easily identified to family level by the following characters: trimerous flowers; two whorls of tepals; three to four whorls of anthers with valvate dehiscence; single carpellate gynoecium bearing an apical ovule; fleshy ellipsoid to globose berries/drupes which may bear a cupule of enlarged receptacular tissue (Rohwer 1993; Eklund 2000). The systematics of the family has long been considered problematic (Kostermans 1957; Reid and Chandler 1933; Mai 1971), and this idea has been corroborated by both morphological studies (Hyland 1989; Li and Christophel 2000), and by molecular phylogenies (Rohwer 2000; Chanderbali et al. 2001; Li et al. 2004, Rohwer and Rudolph 2005). It is evident from recent work that systematic revisions and morphological/anatomical surveys are required in this enigmatic family.

The known fossil record of Lauraceae begins in the early Late Cretaceous with abundant leaves (Crabtree 1987; Kvaček 1992), while reproductive remains such as inflorescences and flowers are less common (Drinnan et al.1990; Crane et al. 1994; Herendeen et al. 1994; Mickle 1996; Eklund and Kvaček 1998; Eklund 1999, 2000; Takahashi et al. 1999, 2001; Frumin et al. 2004). Fossil wood is less common (Herendeen 1991; Poole et al. 2000). Pollen grains are typically not preserved because pollen walls have poorly developed exines (MacPhail 1980; Muller 1981; Herendeen et al. 1994). The Paleogene record is equally abundant, but in contrast to that of Europe, reproductive remains of Lauraceae are rare in North America (Taylor 1988).

Early surveys of the Princeton Chert revealed numerous remains of reproductive structures that were considered to be of lauraceous origin (Sun and Stockey 1991; Penner 1996; Little and Stockey 2003). Immature, but complete inflorescences are described and compared to flowers and inflorescences in the fossil record. Despite the previously mentioned problems with generic circumscriptions among extant Lauraceae, the inflorescences are shown to be distinct from any extant genus. Thus, a new genus and species are erected to accommodate the remains at Princeton, *Similkameena borealis* gen. et sp. nov. Furthermore, due to the abundance of specimens from the Princeton Chert locality, a series of fruits is assembled that represents a developmental sequence from late flowers to mature fruits. This developmental series allows for the amplification of the diagnosis for *Similkameena*, and the anatomical characters seen at different stages of maturity highlight the potential dangers in describing fossil fruits of this family unless developmental characters are elucidated. Such detailed developmental/anatomical data in Lauraceae is currently unknown, illustrating that *Similkameena* is better understood than most extant taxa in terms of its reproductive anatomy and development.

## LITERATURE CITED

BASINGER, J. F. 1976. Permineralized plants from the Eocene Allenby Formation of southern British Columbia. Master's thesis, University of Alberta, Edmonton, Alberta, Canada (unpublished).

BASINGER, J. F., AND G. W. ROTHWELL. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 55: 1984-1990.

BASINGER, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 59: 2379-2410.

BASINGER, J. F. 1984. Seed cones of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 62: 281-289.

BATEMAN, R. M., W. A. DIMICHELE, AND D. A. WILLARD. 1992. Experimental analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: an essay on paleobotanical phylogenetics. *Annals of the Missouri Botanical Garden* 79: 500-559.

BERRY, E. W. 1914. The Upper Cretaceous and Eocene floras of South Carolina and Georgia. *Department of the Interior United States Geological Survey Professional Paper* 84: 1–200.

BERTRAM K. A. 1998. Petrified components of a biotic community from the middle Miocene Virgin Valley Formation, Nevada, USA. Master's thesis, Arizona State University, Tempe, Arizona, USA (unpublished).

BONEHAM, R. F. 1968. Palynology of three Tertiary coal basins in south central British Columbia. Ph.D. thesis, University of Michigan, Ann Arbor, Michigan, USA.

CEVALLOS-FERRIZ, S. R. S., AND R. A. STOCKEY. 1988. Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Lythraceae. *Canadian Journal of Botany* 66: 303–312.

CEVALLOS-FERRIZ, S. R. S., R. A. STOCKEY, AND K. B. PIGG. 1991. The Princeton chert: evidence for *in situ* aquatic plants. *Review of Palaeobotany and Palynology* 70: 173-185.

CHANDERBALI, A. S., H. VAN DER WERFF, AND S. S. RENNER. 2001. Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104-134.

CHANDLER, M. E. J. 1961. Flora of the Lower Headon Beds of Hampshire and the Isle of Wight. *Bulletin of the British Museum (Natural History) Geology* 5: 93–157.

CONTI, E., A. LITT., AND K. J. SYTSMA. 1996. Circumscription of Myrtales and their relationships to other rosids: evidence from rbcL sequence data. *American Journal of Botany* 83:221–233.

CONTI, E., A. LITT, P. G. WILSON, S. A. GRAHAM, B.G. BRIGGS, L. A. S. JOHNSON, AND K. J. SYTSMA. 1997. Interfamilial relationships in Myrtales: molecular phylogeny and patterns of morphological evolution. *Systematic Botany* 22: 629–647.

CRABTREE, D. R. 1987. Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. *Annals of the Missouri Botanical Garden* 74: 707–747.

CRANE, P. R. 1984. Misplaced pessimism and misguided optimism: a reply to Mabberly. *Taxon* 33: 79-82.

CRANE P. R. 1985b. Phylogenetic relationships in seed plants. *Cladistics* 1: 329-348

CRANE P. R. 1985a. Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Garden* 72: 716-793

CRANE, P.R., AND R.A. STOCKEY. 1985. Growth and reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the Late Paleocene of Alberta, Canada. *Canadian Journal of Botany* 63: 340-364.

CRANE P. R., E. M. FRIIS, AND K. R. PEDERSEN. 1994. Palaeobotanical evidence on the early radiation of magnoliid angiosperms. *Plant Systematics and Evolution Supplement* 8: 51–72.

CRANE, P. R., P. HERENDEEN, AND E. M. FRIIS. 2004. Fossils and plant phylogeny. *American Journal of Botany* 91: 1683-1699.

CREPET, W. L., K. C. NIXON, AND M. A. GANDOLFO. 2004. Fossil evidence and phylogeny: the age of major angiosperm clades based on mesofossil and macrofossil evidence from Cretaceous deposits. *American Journal of Botany* 91: 1666-1682.

DILCHER, D.L. 2000. Toward a new synthesis: major evolutionary trends in the angiosperm fossil record. *Proceedings of the National Academy of Science* 97: 7030-7036.

DIMICHELE, W. A. 1985. The upward look in Paleobotany. *Paleobiology* 11: 356-359.

DONOGHUE, M. J., J. A. DOYLE, J. GAUTHIER, A. G. KLUGE, AND T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. *Annual Review of Ecology and Systematics* 20: 431-460.

DRINNAN, A. N., P. C. CRANE, E. M. FRIIS, AND K. R. PEDERSEN. 1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of Eastern North America. *Botanical Gazatte* 151: 370-384.

EKLUND, H. 1999. Big survivors with small flowers: fossil history and evolution of Laurales and Chloranthaceae. Ph.D. thesis Uppsala, Uppsala University, Sweden.

EKLUND, H. 2000. Lauraceous flowers from the Late Cretaceous of North Carolina, U.S.A. *Botanical Journal of the Linnean Society* 132: 397–428.

EKLUND, H., AND J. KVAČEK. 1998. Lauraceous inflorescences and flowers from the Cenomanian of Bohemia (Czech Republic, Central Europe). *International Journal of Plant Sciences* 159: 668–686.

ELLMORE, G. S. 1981. Root dimorphism in *Ludwigia peploides* (Onagraceae): structure and gas content of mature roots. *American Journal of Botany* 68: 557–568.

FELSENSTEIN, J. 2004. Inferring phylogenies. Sinauer Associates Inc. Sunderland MA.

FRIIS, E. M. 1985. Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark). *Biologiske Skrifter, Det Kongelige Danske Videnskabernes Selskab* 24: 1–165.

FRUMIN, S., H. EKLUND, and E. M. FRIIS. 2004. *Mauldinia hirsuta* sp. nov., a new member of the extinct genus *Mauldinia* (Lauraceae) from the Late Cretaceous (Cenomanian-Turonian) of Kazakhstan. *International Journal of Plant Sciences* 165: 883-895.

GASTALDO, R. A. 2001. Terrestrial Plants. *In* D. E. G. Briggs, and P. R. Crowther [eds.] Palaeobiology II, 312-315. Blackwell Science Ltd, Maledin, Massachusetts, USA.

GAUTHIER J., A. G. KLUGE, and T. ROWE. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4: 105-209.

GRAHAM, S. A. 1964. The genera of Lythraceae in the southeastern United States. *Journal of the Arnold Arboretum, Harvard Univiversity* 45: 235–251.

GRAHAM, S. A., AND A. GRAHAM. 1971. The geologic history of the Lythraceae. *Brittonia* 23: 335–346.

GRAHAM S. A., J. V. CRISCI, AND P. C. HOCH. 1993. Cladistic analysis of the Lythraceae *sensu lato* based on morphological characters. *Botanical Journal of the Linnean Society* 113: 1-33.

GRAHAM S. A., R. F. THORNE, AND J. L. REVEAL. 1998. Validation of subfamily names in Lythraceae. *Taxon* 47: 435-436.

GRAHAM, S. A., J. HALL, K. SYTSMA, AND S. SHI. 2005. Phylogenetic analysis of Lythraceae based on four gene regions and morphology. *International Journal of Plant Sciences* 166: 995-1017.

HEER O. 1856. Flora Tertiaria Helvetiae. II. Die apetalen Dicotyledonen. Winterthur, Paris, France.

HERENDEEN, P. S. 1991. Lauraceous wood from the mid-Cretaceous Potomac Group of eastern North America: *Paraphyllanthoxylon marylandense sp. nov*. *Review of Palaeobotany and Palynology* 69: 277-290.

HERENDEEN, P. S., W. L. CREPET, AND K. C. NIXON. 1994. Fossil flowers of Lauraceae from the Upper Cretaceous of New Jersey. *Plant Systematics and Evolution* 189: 29–40.

HERNANDEZ-CASTILLO, G. R. 2006. Systematics of the most ancient conifers. Ph.D. thesis, University of Alberta, Edmonton, Alberta, Canada (unpublished).

HERNANDEZ-CASTILLO, G. R., G. W. ROTHWELL, AND G. MAPES. 2001. Thucydiaceae fam. nov., with a review and reevaluation of Paleozoic walchian conifers. *Interational Journal of Plant Sciences* 162: 1155-1185.

HILTON, J. 2004. Relationships among seed ferns as determined from their seeds. Botanical Society of America meeting, Snowbird, Utah, Abstract 208.

HILTON, H., AND R. M. BATEMAN. 2006. Pteridosperms are the backbone of seed-plant phylogeny. *Journal of the Torrey Botanical Society* 133: 119-168.

HUANG, Y., AND S. SHI. 2002. Phylogenetics of Lythraceae sensu lato: a preliminary analysis based on chloroplast *rbc*L gene, *psa*A-*ycf*3 spacer, and nuclear rDNA internal transcribed spacer (ITS) sequences. *International Journal of Plant Sciences* 163: 215–225.

HULSENBECK, J. P. 1991. When are fossils better than extant taxa in phylogenetic analysis? *Systematic Zoology* 40: 458-469.

HULSENBECK, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* 20: 470-483.

HYLAND, B. P. M. 1989. A revision of Lauraceae in Australia (excluding *Cassytha*) *Australian Systematic Botany* 2: 135-367.

JOHNSON, L. A. S., AND B. G. BRIGGS. 1984. Myrtales and Myrtaceae a phylogenetic analysis. *Annals of the Missouri Botanical Garden* 71: 700-756.

KOEHNE, E. 1903. Lythraceae. *In* A. Engler [ed.], Das Pflanzenreich, Heft 17. IV 216: 1–326. Englemann, Leipzig, Germany.

KOSTERMANS, A. J. G. H. 1957. Lauraceae. *Reinwardtia* 4: 193-256.

KVAČEK, J. 1992. Lauralean angiosperms in the Cretaceous. *Courier Forschungsinstitut Senckenberg* 147: 345–367.

KVAČEK, Z., AND J. SAKALA. 1999. Twig with attached leaves, fruits and seeds of *Decodon* (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds. *Review of Palaeobotany and Palynology* 107: 201-222.

LI, J., AND D. C. CHRISTOPHEL. 2000. Systematic relationships within the *Listea* complex (Lauraceae): a cladistic analysis based on morphological and leaf cuticle data. *Australian Systematic Botany* 13: 1-13.

LI, J., D. C. CHRISTOPHEL, J. G. CONRAN, AND H-W. LI. 2004. Phylogenetic relationships within the 'core' Laureae (*Litsea* complex, Lauraceae) inferred from sequences of the chloroplast gene *mat*K and nuclear ribosomal DNA ITS regions. *Plant Systematics and Evolution* 246: 19-34.

LITTLE, S. A., AND R. A. STOCKEY. 2003. Permineralized fruits of Lauraceae from the Middle Eocene Princeton chert, British Columbia. Botanical Society of America meeting, Mobile, Alabama, Abstract 225.

MACPHAIL, M. K. 1980. Fossil and modern *Beilschmiedia* (Lauraceae) pollen in New Zealand. *New Zealand Journal of Botany* 18: 453-457.

MAI, D. H. 1971. Über fossile Lauraceae und Theaceae in Mitteleuropa. *Feddes Repertorium* 82: 313-341.

MANCHESTER, S. R., D. L. DILCHER, AND S. L. WING. 1998. Attached leaves and fruits of myrtaceous affinity from the Middle Eocene of Colorado. *Review of Palaeobotany Palynology* 102: 153-163.

MANCHESTER, S. R., P. R. CRANE, and L. B. GOLONEVA. 1999. An extinct genus with affinities to extant Davidia and Camptotheca (Cornales) from the Paleocene of North America and eastern Asia. *International Journal of Plant Sciences* 160: 188-207

MATSUMOTO, M., A. MOMOHARA, T. ASAKAWA OHSAWA, AND Y. SHOYA. 1997. Permineralized *Decodon* (Lythraceae) seeds from the Middle Miocene of Hokkaido, Japan, with reference to the biogeographic history of the genus. *Japanese Journal of Historical Botany* 5: 53–65.

MICKLE, J. 1996. *Grexlupus carolinensis*, a new probable lauraceous fruit from the Late Cretaceous of North Carolina. *Journal of the Elisha Mitchell Scientific Society* 112: 1–6.

Moss, P. T., D. R. Greenwood, and S. B. Archibald. 2005. Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia – Washington State) from palynology. *Canadian Journal of Earth Sciences* 42: 187-204.

MULLER, J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1–142.

NIXON, K. C., W. L.CREPET , D. STEVENSON, AND E. M. FRIIS. 1994. A reevaluation of seed plant phylogeny. *Annals of the Missouri Botanical Garden* 81: 484–533.

PIGG, K. P., AND R. A STOCKEY. 1991. Flowers and fruits of *Princetonia allenbyensis* (Magnoliopsida, Family indet.) from the Middle Eocene Princeton Chert of British Columbia. *Review of Paleobotany and Palynology* 70: 163-172.

PIGG, K. P., AND R. A. STOCKEY. 1996. The significance of the Princeton chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. *Washington Geology* 24: 32-36.

PENNER, B. M. 1996. Lauraceous fruit from the Middle Eocene, Princeton Chert (Allenby Formation), British Columbia, Canada. Undergraduate thesis, University of Manitoba, Winnipeg, Manitoba, Canada (unpublished).

POOLE I., H. G. RICHTER, AND J. E. FRANCIS. 2000. Evidence for Gondwanan origins for *Sassafras* (Lauraceae)? Late Cretaceous fossil wood of Antarctica. *International Association of Wood Anatomists Journal* 21: 463–475.

PRYER, K. M., E. SCHUETTPELZ, P. G. WOLF, H. SCHNEIDER, A. R. SMITH, AND R. CRANFILL. 2004. Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *American Journal of Botany* 91: 1582-1589.

REID, E. M., AND M. E. J. CHANDLER. 1933. The London Clay flora. London, England: British Museum (Natural History).

ROBISON, C. R., AND C. P. PERSON. 1973. A silicified semiaquatic dicotyledon from the Eocene Allenby Formation of British Columbia. *Canadian Journal of Botany* 51:

1373–1377.

RODRÍGUEZ-DE LA ROSA, RUBÉN A., S. R. S. CEVALLOS-FERRIZ, AND A. SILVA-PINEDA. 1998. Paleobiological implications of Campanian coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 142: 231–254.

ROHWER, J. G. 1993. Lauraceae. *In* K. Kubitzki, J. G. Rohwer and V. Bittrich [eds.], The families and genera of vascular plants, vol. 2, Flowering plants, dicotyledons: Magnoliid, Hamamelid, and Caryophyllid families, 366–391. Springer Verlag, Berlin, Germany.

ROHWER, J. G. 2000. Toward a phylogenetic classification of the Lauraceae: evidence from *mat*K sequences. *Systematic Botany* 25: 60-71.

ROHWER, J. G., AND B. RUDOLPH. 2005. Jumping genera: the phylogenetic positions of *Cassytha*, *Hypodaphnis*, and *Neocinnamomum* (Lauraceae) based on different analyses of *trn*K intron sequences. *Annals of the Missouri Botanical Garden* 92: 153-178.

ROTHWELL, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review* 65: 188-218.

ROTHWELL, G. W., AND J. F. BASINGER. 1979. *Metasequoia milleri* sp. nov., anatomically preserved pollen cones from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 57: 958-970.

ROTHWELL, G. W., AND R. SERBET. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Systematic Botany* 19: 443-482.

SANDERSON, M. J., J. L. THORNE, N. WILKSTRÖM, AND K. BREMER. 2004. Molecular evidence on plant divergence times. *American Journal of Botany* 91: 1656-1665.

SCHENK, H. 1889. Ueber das Aërenchym, ein dem Kork homologes Gewebe bei Sumpfpflanzen. *Jahrbücher für Wissenschaftliche Botanik, Berlin* 20:526–74.

SCHRENK, J. 1889. On the floating tissue of *Nesaea verticillata* (L.) H.B.K. *Bulletin of the Torrey Botanical Club* 16: 315–323.

SCULTHORPE, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold, London, UK.

SHI, S., Y. HUANG, F. TAN, X. HE, AND D. E. BOUFFORD. 2000. Phylogenetic analysis of the Sonneratiaceae and its relationship to Lythraceae based on ITS sequences of nrDNA. *Journal of Plant Research* 113: 253–258.

SOLTIS, P. S., D. E. SOLTIS, M. J. ZANIS, AND S. KIM. 2000. Basal lineages of angiosperms: relationships and implications for floral evolution. *International Journal of Plant Sciences* 161 (suppl): S97–S107.

STEWART, W. A., AND G. W. ROTHWELL. 1993. Paleobotany and the evolution of plants. 2nd ed. Cambridge University Press, New York, NY.

STOCKEY, R. A. 2001. The Princeton Chert. *In* D. E. G. Briggs, and P. R. Crowther [eds.] Palaeobiology II, 359-362. Blackwell Science Ltd, Maledin, Massachusetts, USA.

STOCKEY, R. A., AND K. B. PIGG. 1994. Vegetative growth of *Eorhiza arnoldii* Robison and Person from the Middle Eocene Princeton chert locality of British Columbia. *International Journal of Plant Sciences* 155: 606-616.

STOCKEY, R. A., AND W. C. WEHR. 1996. Flowering plants in and around Eocene lakes of the interior. *In*: Rolf Ludvigsen [ed.] Life in stone: a natural history of British

Columbia's fossils, 234–247. University of British Columbia Press, Vancouver, British Columbia, Canada.

STOCKEY, R. A., G. W. ROTHWELL, AND A. B. FALDER. 2001. Diversity among taxodiaceous conifers: *Metasequoia foxii* sp. nov. from the Paleocene of central Alberta, Canada. *International Journal of Plant Sciences* 162: 221-234.

SUN, Z., AND R. A. STOCKEY. 1991. Lauraceous inflorescences from the Middle Eocene Princeton Chert (Allenby Formation) of British Columbia, Canada. *American Journal of Botany supplement* 78: Abstract 323.

TAKAHASHI, M., P.R. CRANE, AND H. ANDO. 1999. Fossil flowers and associated plant fossils from the Kamikitaba locality (Ashizawa Formation, Futaba Group, Lower Conianican, Upper Cretaceous) of Northeast Japan. *Journal of Plant Research* 112: 187-206.

TAKAHASHI, M., P. S. HERENDEEN, AND P. R. CRANE. 2001. Lauraceous fossil flower from the Kamikitaba Locality (Lower Coniacian; Upper Cretaceous) in northeastern Japan. *Journal of Plant Research* 114: 429-434.

TAYLOR, D. W. 1988. Eocene floral evidence of Lauraceae: corroboration of the North American megafossil record. *American Journal of Botany* 75: 948-957.

TIFFNEY, B. H. 1981. Fruits and seeds of the Brandon Lignite, VI. *Microdiptera* (Lythraceae). *Journal of the Arnold Arboretum* 62: 487–513.

WEBER, J. L. 1981. A taxonomic revision of *Cassytha* (Lauraceae) in Australia. *Journal of the Adelaide Botanical Garden* 3: 187-262.

WEHR, W. C., AND D. Q. HOPKINS. 1994. The Eocene orchards and gardens of Republic, Washington. *Washington Geology* 22: 27–34.

WOLFE, J. A., and T. TANAI. 1980. The Miocene Seldovia Point flora of the Kenai Group, Alaska. *United States Geological Survey Professional Paper* 1105: 1–52.

**Fig 1.1. Map of Western Canada showing location of Princeton. Map modified from Moss et al. 2005.**

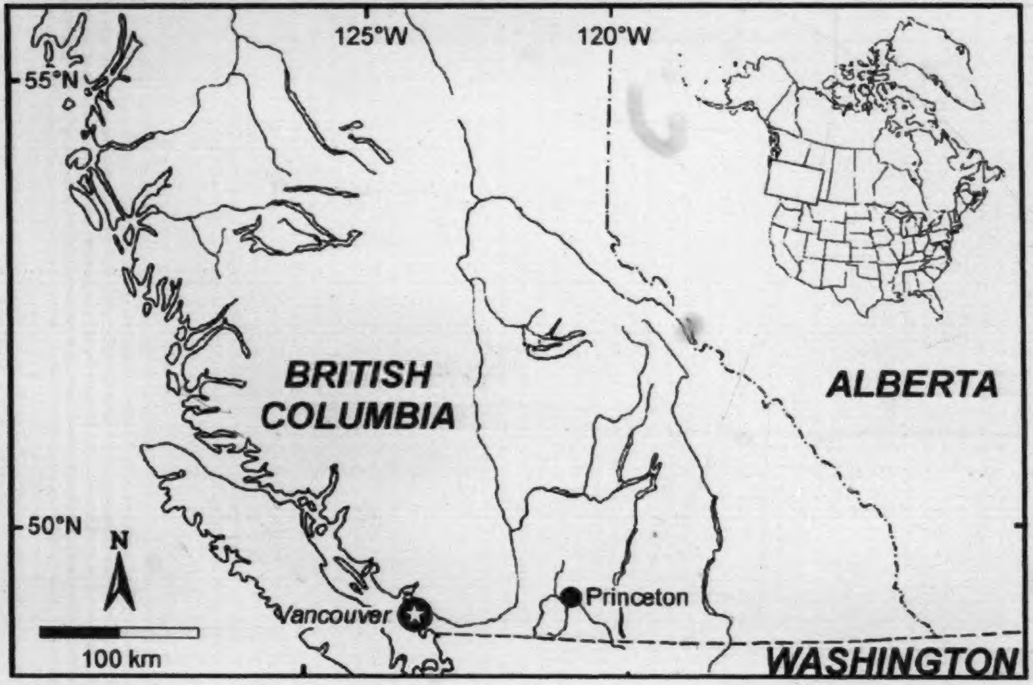
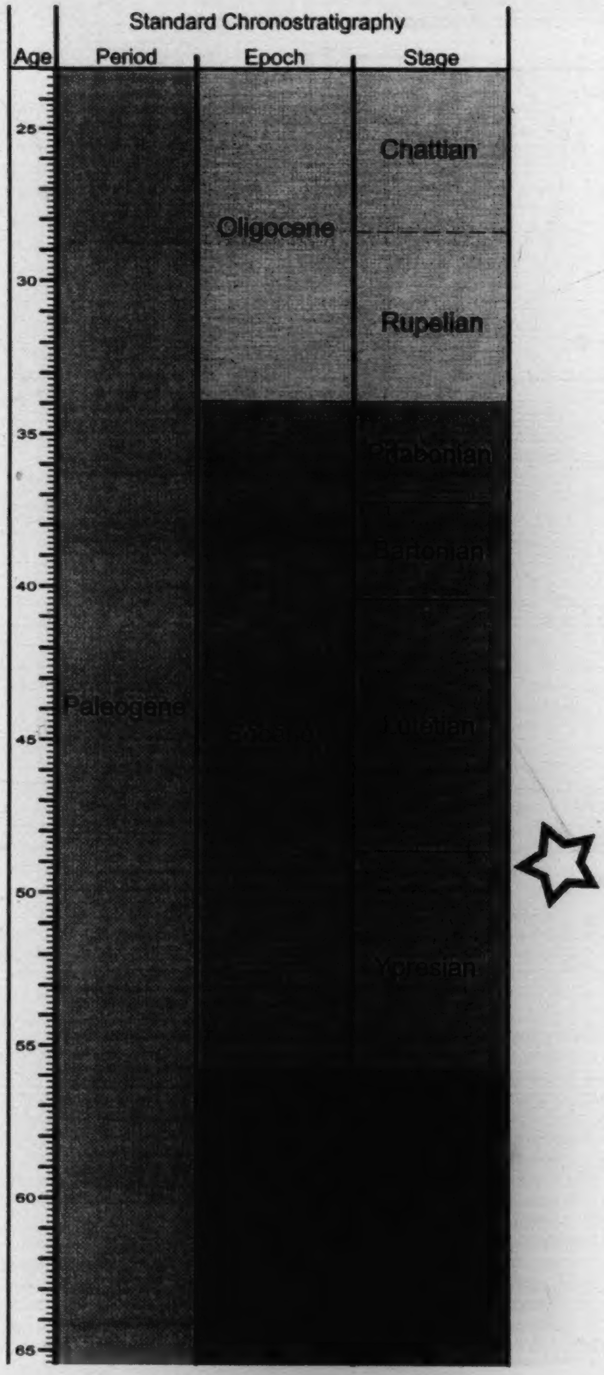


Fig 1.2. Stratigraphic location of the Princeton Chert. Time scale from www.stratigraphy.org



# CHAPTER 2

## Vegetative growth of *Decodon allenbyensis* (Lythraceae) with anatomical comparisons to *Decodon verticillatus*[1]

### INTRODUCTION

Lythraceae is a large tropical to subtropical angiosperm family of 31 genera and 600 species that includes some temperate taxa (Graham 1964). Plants are generally terrestrial, but many are semiaquatic to aquatic (Schrenk 1889; Graham 1964; Sculthorpe 1967; Graham et al. 1993). North American genera include *Ammannia* L., *Cuphea* P. Browne, *Decodon* J.F. Gmelin, *Didiplis* Raf., *Heimia* Link et Otto, *Lythrum* L., *Nesaea* Comm., *Peplis* L., and *Rotala* L. (Conti et al. 1996, 1997; Graham 1999; Judd et al. 1999). Many of these taxa show a tolerance to flooding (Lempe et al. 2001), and one, *Lythrum salicaria* L., is a noxious weed that competitively excludes even hardy species such as *Typha angustifolia* L. in North American wetlands (Mal et al. 1997; Stevens et al. 1997).

The fossil record of Lythraceae is based mainly on dispersed fruits, seeds, and pollen (Graham and Graham 1971; Tiffney 1981). The oldest record of seeds occurs in the Campanian (Cretaceous) of Mexico (Rodríguez-de la Rosa et al., 1998). Vegetative remains of Lythraceae include compression/impression leaves that have been assigned to the genus *Decodon* (Wolfe and Tanai 1980;Wehr and Hopkins 1994; Stockey and Wehr 1996, Kvaček and Sakala 1999). Many myrtalean leaves have similar structure; therefore, it has been suggested that it is not always advisable to assign Paleogene foliage to modern genera in the absence of fruit and flower data (Manchester et al. 1998).

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[1] A version of this chapter has been published. Little and Stockey 2003. International Journal of Plant Sciences. 164: 453-469.

In recent years there have been a number of reports of well-preserved *Decodon* in the fossil record (Cevallos-Ferriz and Stockey 1988; Matsumoto et al. 1997; Bertram 1998; Kvaček and Sakala 1999). To date, the only *Decodon* plant that has been partially reconstructed is *Decodon gibbosus* (E.M. Reid) E.M. Reid ex Nikitin emend. Kvaček et Sakala (1999), based on attached stems, leaves, and fruits from compression fossils found in the Lower Miocene, Bilina Mine, northern Bohemia. Permineralized material from the Miocene of Japan so far has revealed only *Decodon* seeds (Matsumoto et al. 1997), and the Miocene fossil plants, which may include a *Decodon* sp., from the Virgin Valley Formation in Nevada are yet to be described (Bertram and Pigg 1997; Bertram 1998).

The presence of aquatic Lythraceae in the Princeton chert was first recognized by Cevallos-Ferriz and Stockey (1988), who described the permineralized fruits and seeds of *Decodon allenbyensis*. Recently, large numbers of roots, stems, and leaves have been found in the chert in association with fruits and seeds of *D. allenbyensis*. In this study I reconstruct stems and roots of *D. allenbyensis* from the Princeton chert using anatomical comparisons to the only extant *Decodon* species, *Decodon verticillatus* (L.) Ell., and through attachments of roots and stems. One of the ultimate goals of this whole plant reconstruction will be to use *D. allenbyensis* in morphological cladistic analyses, using information from both extant and fossil Lythraceae. These well-preserved lythraceous vegetative remains from the Princeton chert, many found in growth position, also add to our knowledge of growth habit and habitat reconstruction for this fossil *Decodon* species.

## MATERIAL AND METHODS

The permineralized specimens studied here come from the Princeton chert locality situated on the east bank of the Similkameen River, ca. 8.4 km southwest of the town of Princeton, British Columbia (UTM 783724; lat. 49° 22.7' N, long. 120° 32.7' W). This chert outcrop has been called locality "I" (Boneham 1968) and is part of the Allenby Formation in the Princeton Group. There are at least 49 interbedded layers of chert and coal, with an occasional ash bed replacing a chert layer (Stockey 1983; Cevallos-Ferriz et al. 1991), and differing plant associations are found in each chert layer (Pigg and Stockey 1996). The locality is dated as Middle Eocene, based on data from pollen (Rouse and Srivastava 1970), fossil mammals (Russell 1935; Gazin 1953), fish (Wilson 1977, 1982), and potassium-argon gives a date of 48.7 Ma (Lutetian) (Hills and Baadsgaard 1967; H. Baadsgaard, personal communication, 1999).

Chert slabs were peeled with the cellulose acetate peel technique (Joy et al. 1956) modified for hydrofluoric acid (Basinger and Rothwell 1977; Basinger 1981). Several hundred chert blocks from layer 43 were examined for putative *Decodon allenbyensis* Cevallos-Ferriz and Stockey (1988) vegetative material in the University of Alberta Paleobotanical Collection, and the best were chosen for further peeling. Peel sections were mounted with Eukitt rapid mounting medium (O. Kindler, Freiburg, Germany) for microscopic examination.

Extant *Decodon verticillatus* material was obtained from three sources: the margin of Wingfoot Lake, just west of Route 43 between Kent and Hartville, Ohio; Queen's University greenhouses, Kingston, Ontario; and University of Guelph greenhouses, Ontario. This material was embedded and sectioned using standard paraffin techniques (Johansen 1940). Slides were stained with safranin–fast green (Johansen 1940); potassium iodide was used on unstained sections to test for starch. Sections were mounted with standard DPX mounting medium (Electron Microscopy Sciences, Ft. Washington, Pa.). Extant plant samples were prepared for scanning electron microscopy (SEM) after washes in absolute EtOH and dehydration. Critical-point drying used a Polaron apparatus (Waterford, England) for SEM. Roots and leaves were examined by cryo-SEM, using an EMJTECK (K1250) cryosystem.

All woods are studied using the standard procedures for wood descriptions and measurements (IAWA committee 1989). Wood anatomy utilized several axes for both fossil and extant *Decodon*. Because *D. verticillatus* stem wood was described by Baas and Zweypfenning (1979) based on only one 6-mm stem, and root wood was not described, living material was sectioned to provide these descriptions. Measurements of the following specimens were described based on axes of these diameters: *D. verticillatus* stems, 5, 6, and 16 mm; *D. verticillatus*

roots, 4, 7, and 16 mm; *D. allenbyensis* stems, 6 and 10 mm; *D. allenbyensis* roots, 5, 7, and 10 mm. Because of the limitations of techniques using fossils, vessel and fiber lengths are probably conservative, as macerated cells cannot be observed. Observations of *D. verticillatus* wood were performed on sections only to allow for comparable observations; therefore, fiber and vessel lengths are also conservative and probably lack the upper range of these cell lengths. Vesturing classification follows Van Vliet (1978).

Samples for SEM were coated with 150Å gold with a Nanotek sputter-coater and viewed with a JEOL scanning electron microscope (JSM 6301) at 5 kV. Images were taken with a Microlumina (Leaf Systems) digital scanning camera and a Phase One digital studio camera (Phase One A/S, Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe Photoshop 5.5 and 6.0.

## RESULTS

### *Roots*

***Decodon allenbyensis.*** Large numbers of branching roots with lacunate phellem have been identified in the chert (fig. 2.1*a*, 2.1*b*, 2.1*d*; fig. 2.2*a*, 2.2*c*, 2.2*d*). Some specimens show extensive interconnected branching systems with roots of several sizes all surrounded by thin walled phellem (fig. 2.1*a*, 2.1*b*). Others are attached to and arising from stems (figs. 2.1*c*, 2.2*a*). Roots also are observed arising from submerged stems in extant *Decodon verticillatus* (fig. 2.2*b*). In small roots with very little secondary vascular tissue, diameters including phellem tissues range from 0.5 to 15 mm or more, due to the extensive lacunate phellem. Roots in the chert are woody (fig. 2.1*a*, 2.1*d*; fig. 2.2*a*, 2.2*c*, 2.2*d*), and large numbers of small attached roots that lack secondary tissues have also been identified (figs. 2.2*e*–2.2*g*, 2.3*a*).

Primary xylem in young roots is pentarch to hexarch (fig. 2.2*e*, 2.2*f*) to septarch. Primary phloem is not well preserved (figs. 2.2*e*, 2.3*a*). The endodermis and several inner cortical layers are often filled with dark contents in young roots (fig. 2.2*e*, 2.2g; fig.

2.3*a*). In addition, the cortex of young roots is aerenchymatous and the cells often are poorly preserved (fig. 2.2*e*). Epidermal cells are small and rectangular in outline in transverse section (fig. 2.2*e*). A distinctive hypodermis consisting of a single layer of radially elongate cells is present (figs. 2.2*e*, 2.3*a*).

Large numbers of fungal hyphae and circular chlamydospore-like structures occur in the cortical tissues of some of the youngest roots (fig. 2.3*a*, 2.3*b*). The fungi, all well preserved, may represent mycorrhizae or saprophytes and should provide the basis for several further investigations.

Secondary tissues in the fossil roots are well preserved, and there are several distinct growth increments (figs. 2.1*d*, 2.2*c*). Roots that have begun to form secondary xylem have thick-walled fiber bundles in well-preserved secondary phloem (fig. 2.1*d*; fig. 2.2*c*, 2.2*d*; fig. 2.3*c*). These phloem bundles typically range from 156 to 700 µm diameter, and individual fibers are round to polygonal in cross section, with diameters ranging from 39 to 147 µm.

*Fossil root wood description*. Growth rings distinct. Wood diffuse to semi-ring-porous (fig. 2.3*d*). Vessels number ca. (27–)46(–66) $mm^2$, 6%–55% solitary or in radial multiples of 2–5(–7) or rarely in clusters of 3–4, round to oval or tending to angular, tangential diameter (30–)88(–156) µm, radial diameter up to 160 µm; walls 2–4 µm thick. Vessel member length (160–)234(–459) µm. Perforations are simple in oblique end walls (fig. 2.3*i*). Intervessel pits 4–10(–20) µm, crowded, alternate or opposite to reticulate (fig. 2.3*j*), often with reduced borders or with more pronounced border and slit like apertures (fig. 2.4*a*); intervessel pits are vestured (type B1-2) (fig. 2.4*b*), round to polygonal to elongate (figs. 2.3*j*, 2.4*d*). Vessel-ray and vessel-parenchyma pits similar to intervessel pitting, half-bordered and sometimes opposite to scalariform; some rays and axial parenchyma cells with perforations, not easily observed in fossils. Possible tyloses present in some axes (fig. 2.3*k*). Fibers up to 520 μm long, thin walled (2 μm thick) with simple pits, minute and not easily observed, occasionally septate (fig. 2.3*f*, 2.3*g*). Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4(–5) cells. Rays ca. 10 per mm, 1–4(–5)-seriate, heterocellular with upright marginal cells and procumbent to square central cells (fig. 2.3*e*), with occasional sheath cells. Uniseriate rays often completely composed of upright cells with occasional procumbent to square central cells in some rays. Crystals not observable in fossil tissues.

***Decodon verticillatus.*** Young adventitious, aquatic roots of *D. verticillatus* (fig. 2.2*b*) commonly have pentarch or hexarch (fig. 2.4*e*) protosteles, occasionally septarch (fig. 2.4*c*). The endodermis is surrounded by an aerenchymatous cortex (fig. 2.4*h*), a prominent zone of elongate hypodermal cells, and very small epidermal cells (fig. 2.4*c*) as in *D. allenbyensis*. In all respects these roots are similar to those in the fossil material. Roots of extant *D. verticillatus* with secondary tissues produce fiber bundles in the secondary phloem. Size ranges of both the bundles and individual cells are similar to those in the fossil material. Parenchyma cells of the secondary phloem contain abundant druses.

*Extant* D. verticillatus *root wood description*. Growth rings distinct. Wood is diffuse to semi-ring-porous (fig. 2.5*a*). Vessels number ca. (12–)22(–37) $mm^2$, 35%–55% solitary or in radial multiples of 2–5(–6) or rarely in clusters of 3–6, round to oval or tending to angular, tangential diameter (30–)49(–62) μm, radial diameter up to 68 μm, the walls 2–4 μm thick. Vessel member length (132–)245(–430) μm. Perforations are simple in oblique end walls, with rare scalariform perforations found mainly at or near growth increments (fig. 2.4*f*, 2.4*g*). Intervessel pits 4–10(–20) μm, crowded, alternate or opposite to reticulate, often with reduced borders or with more pronounced border and slit-like apertures; intervessel pits vestured (type B1-2), round to polygonal to elongate. Vessel-ray and vessel-parenchyma pits similar, half-bordered, sometimes opposite to scalariform, some ray and most axial parenchyma cells with perforations. Tyloses and vessel contents absent. Fibers up to 612 μm long, thin walled (2 μm thick) with simple minute pits, confined mainly to the radial walls, occasionally septate. Many fiber cells show nuclei and contain abundant oval starch grains. Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4 cells. Rays ca. 10 per mm, 1–4(–6)-seriate, heterocellular with upright marginal cells and procumbent to square central cells (fig. 2.5*b*); rays with occasional sheath cells (fig. 2.5*c*). Uniseriate rays completely composed of upright cells with occasional procumbent to square central cells in some rays. Ray parenchyma cells may contain abundant oval starch grains. Crystals prismatic in ray parenchyma, more commonly in irregular clusters.

### *Phellem*

***Decodon allenbyensis.*** Thin-walled, aerenchymatous, lacunate phellem surrounding woody axes was observed in many of the fossil root specimens (fig. 2.1*a*, 2.1*c*, 2.1*d*; fig. 2.2*d*; fig. 2.6*a*–2.6*d*). Nearly all fossil roots observed, excluding the youngest aerenchymatous roots, possess this lacunate phellem. Phellem is often extensive, up to 4 mm thick, even around small axes (fig. 2.1*a*, 2.1*b*). Concentric layers of several small rectangular, usually dark-colored, cells interrupt the regular pattern of lacunate phellem (fig. 2.2*d*; fig. 2.6*a*, 2.6*c*, 2.6*d*). These bands occur often, and at least 12 such bands of unelongated cells are present around some axes (fig. 2.6*d*). The regular lacunate phellem is composed of radially elongate cells that are T-shaped (fig. 2.6*c*). Small rectangular phellem cells separate the elongate cells, giving the aerenchymatous phellem a crosshatched appearance (fig. 2.6*a*–2.6*d*).

***Decodon verticillatus.*** Lacunate phellem closely resembles that in fossil roots (fig. 2.6*e*, 2.6*f*). This secondary growth is very delicate and spongy and does not maintain its integrity well even in paraffin histology. Cell types are the same as described for the fossil, with radially elongate T-shaped cells. Small rectangular cells separate the elongate cells (fig. 2.6*f*). Consecutive layers of compressed cells are also produced in *D. verticillatus*.

### *Stems*

***Decodon allenbyensis.*** Many stem axes (fig. 2.1*c*; fig. 2.7*a*, 2.7*d*) were observed in close association with the fossil roots with thin-walled phellem. Some of these stems do not show sufficient anatomical characters for identification because of their age and often because of fungal degradation. Without organic connection of these young stems to other organs, it is not known if they represent inflorescence axes or twigs of other taxa. However, some isolated stems show sufficient anatomical characters to link them to the roots, and some are found in attachment.

Pith cells in *D. allenbyensis* are homocellular and are made up of isodiametric, or somewhat axially elongated, cells 20–70 μm in diameter (fig. 2.7*d*). Associated with the outer pith cells is a zone of what appears to be phloem tissue just internal to the wood. Many young stems are decorticated (fig. 2.7*d*); however, some show well-preserved extraxylary primary tissues (fig. 2.7*a*). These young stems have an undulating and angular, often square, outline in transverse section. The cortical cells often have prominent irregular air spaces between them (fig. 2.7*a*). A band of sclerotic cells is found to the outside of the phloem.

In addition to stems with lacunate phellem and adventitious roots, several woody stems were peeled because of their abundance and close association with *D. allenbyensis* roots. In stems with substantial secondary xylem, secondary phloem can also be well preserved (fig. 2.7*i*). Secondary phloem has phloem fiber bundles, similar in size and appearance to those seen in secondary phloem of fossil and extant roots.

*Fossil stem wood description*. Growth rings distinct (fig. 2.7*e*). Wood is diffuse to semi-ring-porous (fig. 2.7*d*, 2.7*e*). Vessels number ca. (25–)46(–86) mm$^2$; 4%–12% are solitary or in radial multiples 2–5(–7) or in clusters of 3–8, round to oval or tending to angular, tangential diameter (28–)70(–130) μm; radial diameter up to 109 μm, walls 2–4 μm thick. Vessel member length (170–)275(–430) μm. Perforations are simple in oblique end walls. Intervessel pits 4–10(–20) μm, crowded, alternate or opposite to reticulate; intervessel pits with reduced borders, vestured (type B1-2) and round to polygonal to elongate. Vessel-ray and vessel-parenchyma pits similar, half bordered, and sometimes opposite to scalariform, not easily observed in fossils. Possible tyloses present in some axes. Fibers up to 571 μm long, thin walled (2 μm thick) with simple fiber pits minute and not easily observed, occasionally septate. Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4 cells. Rays ca. 10 per mm, 1–4(–5)–seriate (fig. 2.7*g*), heterocellular with upright marginal cells and procumbent to square central cells (fig. 2.7*h*); rays with occasional sheath cells. Uniseriate rays completely composed of upright cells with occasional procumbent to square central cells in some rays. Crystals not observable in fossils.

***Decodon verticillatus.*** Younger stems are nearly square or polygonal in cross section (fig. 2.7*c*). *Decodon verticillatus* has mainly opposite but also subopposite to verticillate branching, and leaves are also opposite to verticillate. Pith cells are homocellular and isodiametric or somewhat axially elongate and range from 12 to 92 μm in diameter (figs. 2.7*c*, 2.8*a*). Many of the parenchymatous cells in stems contain druses (fig. 2.8*a*, at arrow). There are irregular, aerenchymatous air spaces between the outer cortical cells in stems of *D. verticillatus* (fig. 2.7*c*), contributing to the shape of the undulating stem margin. A band of sclerotic cells is found to the outside of the phloem and is part of the primary cortex. These primary sclerotic cells are eventually sloughed off along with the cortex, because of phellem production.

Secondary phloem fibers that are produced by woody stems are similar in appearance and size range to those of extant roots and to those of fossil axes (fig. 2.7*b*). Abundant druses are observed in parenchyma cells of the secondary phloem (fig. 2.7*b*).

Stem wood of *D. verticillatus* was described by Baas and Zweypfenning (1979), and additional observations and measurements are reported here. This description adds new observations and extends the ranges of some quantitative measurements.

*Extant stem wood description*. Growth rings distinct. Wood is diffuse to semi-ring-porous (fig. 2.8*c*). Vessels number ca. (39–)60(–84) mm$^2$, 6%–35% solitary or radial multiples of 2–5(–6) (fig. 2.8*c*, 2.8*e*) or rarely in clusters of 3–6, round to oval or tending to angular, tangential diameter (30–)49(–78) μm, radial diameter up to 80 μm, walls 2–4 μm thick. Vessel member length (109–)240(–490) μm. Perforations are simple in oblique end walls (fig. 2.7*k*; fig. 2.8*b*, 2.8*d*). Intervessel pits 4–10(–20) μm, crowded, alternate or opposite to reticulate, often with reduced borders or with more pronounced border and slit-like apertures; intervessel pits are vestured (type B1-2) (fig. 2.8*d*, 2.8*f*), round to polygonal to elongate. Vessel-ray and vessel-parenchyma pits similar, half-bordered, and sometimes opposite to scalariform, ray and axial parenchyma cells rarely with perforations (observed only once out of several sections). Tyloses and vessel contents absent. Fibers up to 632(–700) μm (Baas and Zweypfenning 1979) long, thin walled (2 μm thick), with simple, minute pits, confined mainly to radial walls, occasionally septate. Many fiber cells show nuclei and contain abundant oval starch grains. Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4(–6) cells. Rays ca. 10 per mm, 1–4(–6)–seriate (fig. 2.7*j*), heterocellular with upright marginal cells and procumbent to square central cells (fig. 2.7*f*), with occasional sheath cells. Uniseriate rays often completely composed of upright cells with occasional procumbent to square central cells in some rays. Ray parenchyma cells may contain abundant oval starch grains. Crystals prismatic in ray parenchyma, often found as irregular clusters.

### *Habit*

***Decodon allenbyensis.*** Large, sometimes partially crushed, axes exist with as many as 18 growth increments. They were at least 5–15 cm in diameter in life. Axes tend to be found in a horizontal orientation, near or dipping away from the coal at the top of the chert layer. The longest such axis known extends obliquely and completely through a 28.5-cm chert block. Typical branching root systems that produce delicate lacunate phellem are observed arising and extending downward from stems and these large prostrate axes.

## DISCUSSION

Woody dicot roots with lacunate phellem are among the most common remains in layer 43 of the Princeton chert. Other vascular plants in this layer include two types of monocot seeds and several monocot vegetative organs. Dicot remains include seeds or crushed axes of *Eorhiza arnoldii* Robison and Person (1973) and seeds of *Allenbya collinsonae* Cevallos-Ferriz and Stockey (1989), Nymphaeaceae. Both of these taxa are rare in layer 43, and their vegetative remains are either known or unlikely to be similar to the vegetative material described here. Among the most common dicot remains are two myrtalean taxa based on fruits and seeds: *Decodon allenbyensis* Cevallos- Ferriz and Stockey (1988), Lythraceae, and *Paleomyrtinaea princetonensis* Pigg et al. (1993), Myrtaceae. The stems and roots described here, like many plants at Princeton, are *in situ* aquatics preserved in growth position (Cevallos-Ferriz et al. 1991). Therefore, one would expect all of the organs of this plant to be present in the layer.

Spongy, aerenchymatous tissues like those found in the fossil are also produced by several semiaquatic Lythraceae, Melastomataceae, Onagraceae, Fabaceae, and Euphorbiaceae (Schenck 1889). However, general wood features of the fossil, such as vestured pits and intraxylary phloem, exclude Fabaceae and Euphorbiaceae and may indicate that the roots and stems investigated in this study are those of a member of Myrtales (Van Vliet and Baas 1984). Broad wood anatomical patterns in Myrtales are discussed in depth by Van Vliet and Baas (1984), and this study helped exclude many families and subfamilies for the fossil wood.

The fossil wood described here has vessels in radial multiples and lacks fiber tracheids. Within Myrtales, Penaeaceae; Melastomataceae, subfamily Memecyloideae and Combretaceae, subfamily Strephonematoideae have wood with exclusively solitary vessels, or nearly so, that co-occur with fiber tracheids (Van Vliet and Baas 1984). Vessels in radial multiples occur in Melastomataceae, subfamily Crypteronioideae, but these taxa also have fiber tracheids (Van Vliet and Baas 1984). Combretaceae, subfamily Combretoideae, while they can have vessels in radial multiples and scanty paratracheal parenchyma, like the fossils, Combretoideae also have aliform, banded, or confluent and infrequently marginal parenchyma, mostly uniseriate rays composed of mainly procumbent cells, and large idioblasts in ray and axial parenchyma (Van Vliet 1978; Van Vliet and Baas 1984). These axial parenchyma patterns, rays, and idioblasts are absent from the fossil wood.

Vegetative remains of Myrtaceae are likely to occur in layer 43 because of the presence of fruits and seeds of *P. princetonensis*. Myrtaceous wood typically has solitary vessels, often forming oblique patterns. *Xanthomyrtus* Diels (subfamily Myrtoideae), *Eucalyptopsis* C.T. White, and *Eucalyptus* L'Herit. (subfamily Leptospermoideae), however, have vessels in radial multiples and lack fiber tracheids (Van Vliet and Baas 1984), like the fossil wood. These genera have aliform to confluent wood parenchyma (Van Vliet and Baas 1984), in contrast to the fossil wood with scanty paratracheal parenchyma. Thus, it is unlikely that these axes represent the vegetative remains of *P. princetonensis* or other Myrtaceae.

*Heteropyxis* Harv. and *Psiloxylon* Thou. ex Tul. have been placed historically in various orders and families, including Myrtaceae, based on detailed morphological characters (Schmid 1980). Based on *rbc*L sequence data, these two genera have been included in a clade that contains Myrtaceae and Vochysiaceae (Conti et al. 1997). *Heteropyxis* is reported to lack axial parenchyma, and both *Heteropyxis* and *Psiloxylon* have fibers with distinctly bordered pits (Schmid 1980), differing from the fossil wood with scanty paratracheal parenchyma and libriform fibers. However, *Psiloxylon* is also reported to have fibers with minute pits (Van Vliet and Baas 1984). In Vochysiaceae, axial parenchyma is vasicentric or commonly in paratracheal bands (Cronquist 1981), whereas the fossil wood has scanty paratracheal parenchyma. These taxa are unlikely to be related to the fossil plant since they are not aquatics nor are they reported to produce spongy lacunate phellem.

In the Conti et al. (1997) *rbc*L gene tree, the genera *Rhynchocalyx* Oliver, *Alzatea* Ruiz & Pav., *Olinia* Thunb., and *Penaea* L. form a clade sister to the Melastomataceae, and *Rhynchocalyx* and *Alzatea* appear as sister groups, based on the morphological analysis of Johnson and Briggs (1984). *Rhynchocalyx*, *Alzatea* and *Olinia*, each in a monogeneric family, have wood anatomy similar to Lythraceae, and wood descriptions for *Rhynchocalyx* and *Alzatea* were included in Lythraceae (Van Vliet and Baas 1984). However, these African and Central to South American taxa are trees or shrubs and are not reported to be aquatics (Cronquist 1981; Graham 1984; Johnson and Briggs 1984). In addition, *Rhynchocalyx* has thin-walled fibers surrounding the vessels; *Alzatea* has coarse, elongated, simple vessel-ray pits (Baas 1979; Baas and Zweypfenning 1979). Therefore, these genera are unlikely to be closely related to the fossil plant.

Some Melastomataceae have been reported to produce aerenchyma from a phellogen (Schenk 1889). *Rhynchanthera dichotoma* DC and *Acisanthera variabilis* Triana have phellem similar to that produced by extant *Decodon* and the fossil plant. The fossil wood has already been excluded from subfamilies Memecyloideae and Crypteronioideae (see discussion toward the beginning of this section). Subfamily Melastomatoideae has alternate, plus elongate and curved or scalariform intervessel pitting. Fibers in this subfamily also tend to be dimorphic, where some fibers appear parenchyma-like and are distributed in narrow tangential arcs or in confluent and banded patterns (Van Vliet and Baas 1984). The fossil plant is unlikely to be a member of Melastomataceae, since this type of intervessel pitting and fiber type are absent in the wood.

Onagraceae and Lythraceae are sister groups in the Conti et al. (1997) *rbc*L phylogenetic study and have very similar basic wood anatomy (Van Vliet and Baas 1984). Many Onagraceae are herbaceous or only produce small amounts of secondary xylem (Carlquist 1975); however, some taxa may be shrubs and small trees, e.g., *Ludwigia anastomosans* (DC) Hara (Carlquist 1987). The Onagraceae also has aquatic taxa that produce lacunate phellem. Some species of Onagraceae have included phloem, and some also have elongate and curved intervessel pitting, but this is not common to all taxa in the family (Carlquist 1975, 1977, 1982, 1987). Some species of *Ludwigia* L. lack both of these wood characters, having wood similar to Lythraceae. Therefore, the presence of lacunate phellem and similarity of wood characters in both Lythraceae and Onagraceae make identification of the fossil to one or the other of the families difficult, even though certain characters, such as included phloem and irregular curved intervessel pitting, exclude many Onagraceae.

Most Onagraceae that do produce aerenchyma do not show the same cellular organization in this tissue as in the fossil. However, some species of *Ludwigia* (= *Jussiaea*) are reported to have spongy lacunate phellem produced on submerged axes (Schenck 1889). Ellmore (1981) states that *Ludwigia peploides* (Kunth) P.H. Raven only produces true lacunate phellem on lateral submerged stems that grow out across the water. The downward-growing adventitious roots arising from lateral submerged stems do not produce aerenchymatous tissues (Ellmore 1981). A tissue similar to lacunate phellem, presumed to improve aeration to the submerged organs, is produced by upward-growing adventitious roots (Ellmore 1981). The aerenchyma of these upward-growing roots was observed by Ellmore (1981) to be derived from the regular radial elongation of primary cortical cells, emulating the organized pattern of lacunae seen in aerenchyma derived from a phellogen. Schenck (1889) also reports that aerenchyma is produced from the "*primäre Rindenparenchym*" (primary cortex) in the submerged adventitious roots of *Ludwigia* spp. Upward-growing roots do not produce true phellem or secondary xylem (Ellmore 1981; Schenck 1889). All our fossil roots appear to have been downward growing, and all lacunate tissues are produced by a phellogen on roots with secondary xylem. Schenck (1889) reports that downward-growing roots of other *Ludwigia* species, however, do produce lacunate phellem.

Downward-growing roots in Onagraceae that become aerenchymatous begin by producing lacunate, phellem-like tissue derived from primary cortex in the same way as upward-growing roots. However, these roots will eventually begin producing true lacunate phellem from a phellogen arising in the pericycle (Schenck 1889; Ellmore 1981). It is clear from our observations of the fossil roots and those of *Decodon verticillatus* that the primary cortex produces a network of air spaces within the bounds of the epidermis, and a true phellogen-producing lacunate phellem is the only source of the organized crosshatched aerenchyma. The fossil roots probably produced a phellogen in the pericycle, as in extant *D. verticillatus*, that co-occurs with secondary vascular tissue production. This developmental pattern in downward-growing roots is not known in Onagraceae.

Within Lythraceae aerenchymatous tissue produced by a phellogen on submerged axes has been reported for *Lythrum* L., *Peplis* L., *Ammannia* L., *Cuphea* P. Browne, *Heimia* Link et Otto, *Pleurophora* D. Don, and *Decodon* J.F. Gmelin (Schrenk 1889; Graham 1964; Sculthorpe 1967; Stevens et al. 1997; Lempe et al. 2001). *Peplis* is an herbaceous genus (Graham 1964) and is therefore unlike the woody fossil. *Ammannia* is generally thought of as herbaceous but produces small amounts of wood (Baas and Zweypfenning 1979). *Ammannia* has non-septate fibers and unseriate rays, differing from the fossil that has septate fibers and multiseriate rays. *Cuphea* usually also has uniseriate rays, except for *Cuphea speciosa* (Anders.) Kuntze that has 1–4-seriate rays (Baas and Zweypfenning 1979). However, in *Cuphea* the axial parenchyma is in strands of one or two cells, unlike the fossil that has axial parenchyma in strands of two to four cells. *Heimia* and *Pleurophora* produce lacunate phellem with cells elongating in an irregular pattern (Schrenk 1889; Lempe et al. 2001), differing from the regular appearance of the fossil phellem. *Pleurophora* and *Heimia* have vascular tracheids, and *Heimia* also has wellmarked spiral thickenings on the tracheary elements (Baas and Zweypfenning 1979; Baas 1986). Vascular tracheids and spiral thickenings on tracheary elements are not observed in the fossil wood.

The only other taxa of Lythraceae known to produce similar spongy tissue to the fossil are *Lythrum* and *Decodon*. There are no known qualitative differences reported by Lempe et al. (2001) in the structure of the lacunate phellem produced by *Lythrum* spp. and *D. verticillatus*, both with phellem similar to the fossil. However, Schrenck (1889) observed occasional concentric layers of compact suberized cells in the phellem of *D. verticillatus*. He suggested that these suberized layers prevent aeration of submerged axes since the suberized cell layers would seal off the stem from both the environment and the inner axis. He suggested, therefore, that the lacunate phellem was important for flotation. These suberized layers were observed in this study for both living *Decodon* and the fossil plants and are interpreted to be evidence of consecutive phellogens. This sort of occasional compact cell layer is not reported in *Lythrum* (Schrenck 1889). The production of consecutive phellogens may contribute to the ability of the *Decodon* to produce large amounts of lacunate phellem.

The wood anatomy in *Lythrum* spp. is very similar to *Decodon*, but *Lythrum* differs in having exclusively uniseriate rays and occasionally unilaterally compound vessel-ray and vessel-parenchyma pitting (Baas and Zweypfenning 1979). The fossil and *D. verticillatus* often have bi- to triseriate or wider rays and lack unilaterally compound vessel-ray and vessel-parenchyma pitting.

When comparing fossil axes with those of extant *D. verticillatus*, similarities are obvious. Both plants possess young adventitious roots that have pentarch to septarch primary xylem, with an aerenchymatous cortex and a radially elongate hypodermal layer. The fossil and extant plants possess large fiber bundles in secondary phloem and multiple phellogens that produce lacunate phellem on submerged roots and stems. Pith cells are of similar size and shape, and primary cortical tissues are similar in both taxa.

Fungi are particularly abundant within these fossil plant remains and within the chert in general (Currah and Stockey 1991; LePage et al. 1994, 1997; Hill-Rackette et al. 1995; Currah et al. 1998). Similar structures were not observed in young extant roots. There is a possibility that the large number of hyphae and chlamydospore-like structures found in the youngest roots in the chert represent mycorrhizal fungi, as have been reported in other Lythraceae (K. J. Stevens, personal communication, 1999).

Secondary xylem in *D. verticillatus* and the fossil have similar qualitative characters including distinct growth rings, diffuse to semi-ring-porous wood, vessels with simple perforations, vessels in radial multiples of two to five, similar intercellular pitting patterns, type B1-2 vesturing on intervessel pits, septate fibers, scanty paratracheal axial parenchyma in strands of two to four, and number of rays per square millimeter. Both taxa have root wood with some intervessel pits that have slit like apertures. Perforated axial parenchyma and rare perforated ray parenchyma in the root wood of extant *D. verticillatus* are also present in the fossil root wood although they are difficult to observe. Perforated axial parenchyma is a new character within Lythraceae and appears unique to the fossil and extant *Decodon*.

The fossil wood and the wood of *D. verticillatus* differ in some qualitative characters. Fossil axes possess tyloses, whereas extant *D. verticillatus* lacks tyloses. Extant *Decodon* root wood has occasional scalariform perforations, while scalariform perforations were not seen in vessel elements of the fossil root wood.

There are quantitative differences between the root wood and the stem wood of *D. verticillatus* in vessel widths, vessel density, and percentage of grouped vessels. *Decodon verticillatus* has more solitary vessels and fewer per square millimeter in its roots than in its stems. It is important to note that *D. verticillatus* stem material, studied in depth for wood anatomy, came from a wild population growing on the margin of Wingfoot Lake (near Kent, Ohio), in contrast to the root material that came from greenhouse-grown plants. Greenhouse plants grew in soil and had regular watering, whereas wild-grown plants were subjected to fluctuation in water levels as they grew on the margin of the lake. Increasing vessel grouping and vessel density in wood during times of increased water stress may prevent embolisms in woods that lack tracheids associated with vessels (Carlquist 1988). In greenhouse-grown plants, root wood vessel width is narrower than that in stems from plants growing near the lake. Greenhouse conditions would not have given the plants access to a large volume of water at any one time. Therefore, they would have been unable to produce vessels as wide as a submerged plant. Wood with narrower vessels is less efficient in water conduction, but plants are less likely to develop embolisms (Ewers 1985).

The fossil roots and stems have a less pronounced difference in the vessel densities. However, the fossil wood shows a marked increase in the proportion of vessels in groups for the stems versus roots. Vessel diameter tends to be wider in the roots compared with diameters in stems. Vessels are expected to be longer and wider in the roots than in the stems of a given species (Carlquist 1978). Since the roots observed were submerged in water, it would be expected that these axes would be under little water stress. However, the stems are farther away from the water source, and therefore one would expect them to have anatomical adaptations to mitigate the effects of water stress. Increasing the percentage of grouped vessels allows for adjacent vessels to maintain the water column in case of an embolism (Carlquist 1988). The similarity of vessel density in the fossil roots and stems may indicate that water levels were steady over the growing season.

There are differences between extant and fossil plants in percent vessel grouping, vessel density, and vessel width. However, the ranges of these values overlap between the fossil and extant woods. Therefore, these differences in wood anatomy were treated as evidence of minor environmental variations. These data indicate that, compared with the extant plants sectioned for comparison, the fossil plants grew in stable water levels.

The fossil axes described here are considered to be those of *Decodon* because of the anatomical and developmental characters shared with living *D. verticillatus*. In addition, Baas and Zweypfenning (1979, p. 122) note that within Lythraceae, *D. verticillatus* has relatively large ray cells, "creating a characteristic histology as seen in transverse and tangential sections." Although this is a somewhat subjective character, in this study, the ray cells in the fossil wood are also large, causing the rays to look quite prominent in transverse and tangential sections. In particular, these fossil *Decodon* axes are considered to be the vegetative organs belonging to *D. allenbyensis* because of the abundance and close association of these *in situ* preserved axes with the fruits and seeds of *D. allenbyensis*.

The growth habit of the fossil appears to have been similar in all respects to that of living *D. verticillatus*. This plant probably grew near the water's edge, forming procumbent stems over the water, spongy buoyant phellem, and adventitious roots growing down into the water, as is seen in the only extant species of *Decodon* (Graham 1964; Sculthorpe 1967). The fossil plants also probably formed similar thickets in and around the water margin.

*Decodon allenbyensis* has axes with up to 18 growth increments that are at least 5–15 cm in diameter. In contrast, the "typical" stems of extant *D. verticillatus* (S. A. Graham, personal communication, 2002) range from 2 to 4 cm in diameter, including several branching roots. In more established populations or populations growing in warmer climates, stems may get significantly wider (C. Eckert, personal communication, 2002). However, upper ranges of diameters for *D. verticillatus* have not been recorded or published. Therefore, it can only be concluded that the fossil *D. allenbyensis* may have been a larger plant than *D. verticillatus*, but at the very least, the fossil was a well established plant, producing substantial wood.

Morphological cladistic analyses of Lythraceae (Graham et al. 1993) and molecular cladistic analysis using *cp*DNA (Conti et al. 1997) show that relationships are not clear within this family. Even with the addition of *nr*DNA ITS and *psaA-ycf3* spacer sequence data, some of the relationships in Lythraceae are still not well supported (Shi et al. 2000; Huang and Shi 2002). Therefore, *D. allenbyensis* may provide invaluable data for future analyses and phylogenetic understanding of Lythraceae.

Leaves have not yet been found attached to *D. allenbyensis* stems, but large numbers of dicot leaves have been found in close association with stems and roots (Little and Stockey 2002) and are the subject of chapter 4. The more complete plant reconstruction will be more useful in cladistic analyses (Huelsenbeck 1991).

*Decodon allenbyensis* adds to the detailed and rich data set already known for the Princeton chert. The characteristic aquatic anatomy of the plant provides additional evidence that this locality preserves a wetland community of the Middle Eocene.

Cevallos-Ferriz et al. (1991) discussed the aquatic nature of the Princeton chert and summarized the numerous plants that were growing in place and preserved *in situ*. The excellent preservation of abundant delicate lacunate phellem of *D. allenbyensis* supports the argument that this species was preserved *in situ*. *Decodon allenbyensis* probably displayed a similar life history pattern to extant *Decodon*, rooting at the margin of a quiet body of fresh water and growing out over the surface.

## LITERATURE CITED

Baas P 1979 The anatomy of *Alzatea* Ruiz & Pav (Myrtales). Acta Bot Neerl 28:156–158.

——— 1986 Wood anatomy of Lythraceae: additional genera (*Capuronia, Galpinia*, Haitia, *Orias*, and *Pleurophora*). Ann Mo Bot Gard 73:810–819.

Baas P, RCVJ Zweypfenning 1979 Wood anatomy of the Lythraceae. Acta Bot Neerl 28:117–155.

Basinger JF 1981 The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. Can J Bot 59:2379–2410.

Basinger JF, GW Rothwell 1977 Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. Can J Bot 55:1984–1990.

Bertram KA 1998 Petrified components of a biotic community from the middle Eocene Virgin Valley Formation, Nevada, USA. MS thesis. Arizona State University, Tempe.

Bertram KA, KB Pigg 1997 Middle Miocene flora from the Virgin Valley, northwestern Nevada, USA. Am J Bot 84 (suppl):129.

Boneham RF 1968 Palynology of three Tertiary coal basins in south central British Columbia. PhD diss. University of Michigan, Ann Arbor.

Carlquist S 1975 Wood anatomy of Onagraceae: further species: root anatomy: significance of vestured pits and allied structures in dicotyledons. Ann Mo Bot Gard 69:755–769.

——— 1977 Wood anatomy of Onagraceae: additional species and concepts. Ann Mo Bot Gard 64:627–637.

——— 1978 Wood anatomy and relationships of Bataceae, Gyrostemonaceae, and Stylobasiaceae. Allertonia 5:297–330.

——— 1982 Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. Ann Mo Bot Gard 62:386–424.

——— 1987 Wood anatomy of noteworthy species of *Ludwigia* (Onagraceae) with relation to ecology and systematics. Ann Mo Bot Gard 74:889–896.

——— 1988 Comparative wood anatomy. Springer, Berlin. 436 pp.

Cevallos-Ferriz SRS, RA Stockey 1988 Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Lythraceae. Can J Bot 66: 303–312.

——— 1989 Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Nymphaeaceae. Bot Gaz 150:207–217.

Cevallos-Ferriz SRS, RA Stockey, KB Pigg 1991 The Princeton chert: evidence for *in situ* aquatic plants. Rev Palaeobot Palynol 70:173–185.

Chandler MEJ 1961 Flora of the Lower Headon Beds of Hampshire and the Isle of Wight. Bull Br Mus (Nat Hist) Geol 5:93–157.

Conti E, A Litt, KJ Sytsma 1996 Circumscription of Myrtales and their relationships to other rosids: evidence from *rbc*L sequence data. Am J Bot 83:221–233.

Conti E, A Litt, PG Wilson, SA Graham, BG Briggs, LAS Johnson, KJ Sytsma 1997 Interfamilial relationships in Myrtales: molecular phylogeny and patterns of morphological evolution. Syst Bot 22:629–647.

Cronquist A 1981 An integrated system of classification of flowering plants. Columbia University Press, New York. 1262 pp.

Currah RS, RA Stockey 1991 A fossil smut fungus from the anthers of an Eocene angiosperm. Nature 350:698–699.

Currah RS, RA Stockey, BA LePage 1998 An Eocene tar spot on a fossil palm and its fungal hyperparasite. Mycologia 90:667–673.

Ellmore GS 1981 Root dimorphism in *Ludwigia peploides* (Onagraceae): structure and gas content of mature roots. Am J Bot 68:557–568.

Ewers FW 1985 Xylem structure and water conduction in conifer trees, dicot trees, and lianas. IAWA (Int AssocWood Anat) Bull, NS, 6:309–317.

Gazin CL 1953 The Tillodontia: an early Tertiary order of mammals. Smithson Misc Collect 1221:1–110.

Graham A, SA Graham 1971 The geologic history of the Lythraceae. Brittonia 23:335–346.

Graham SA 1964 The genera of Lythraceae in the southeastern United States. J Arnold Arbor Harv Univ 45:235–251.

——— 1984 Alzateaceae: a new family of Myrtales in the American tropics. Ann Mo Bot Gard 71:757–779.

——— 1999 The emerging picture of Lythraceae: cladistic analysis of morphological and cpDNA characters. XVI International Botanical Congress Abstracts 20:250.

Graham SA, JV Crisci, PC Hoch 1993 Cladistic analysis of the Lythraceae *sensu lato* based on morphological characters. Bot J Linn Soc 113:1–33.

Hill-Rackette GL, RS Currah, RA Stockey 1995 A fungal blight on the fruits of an Eocene aquatic dicot. Am J Bot 82 (suppl):86.

Hills LV, H Baadsgaard 1967 Potassium-argon dating of some lower Tertiary strata in British Columbia. Bull Can Petrol Geol 15:138–149.

Huang Y, S Shi 2002 Phylogenetics of Lythraceae *sensu lato*: a preliminary analysis based on chloroplast *rbc*L gene, *psaA-ycf3* spacer, and nuclear rDNA internal transcribed spacer (ITS) sequences. Int J Plant Sci 163:215–225.

Huelsenbeck, JP1991 When are fossils better than extant taxa in phylogenetic analyis? Syst Zoo 40: 45-469.

IAWA Committee (Wheeler, EA, P Baas, P Gasson eds.) 1989 IAWA list of microscopic features for hardwood identification. IAWA 10: 219-332.

Johansen DA 1940 Plant microtechnique. McGraw-Hill, New York. 523 pp.

Johnson LAS, BG Briggs 1984 Myrtales and Myrtaceae: a phylogenetic analysis. Ann Mo Bot Gard 71:700–756.

Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in palaeobotany. Ann Bot (London), NS, 20:635–637.

Judd WS, CS Campbell, EA Kellogg, PF Stevens 1999 Plant systematics: a phylogenetic approach. Sinauer, Sunderland, Mass. 423 pp.

Kvaček Z, J Sakala 1999 Twig with attached leaves, fruits and seeds of *Decodon* (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds. Rev Palaeobot Palynol 107:201–222.

Lempe J, KJ Stevens, RL Peterson 2001 Shoot responses of six Lythraceae species to flooding. Plant Biol 3:186–193.

LePage BA, RS Currah, RA Stockey 1994 The fossil fungi of the Princeton chert. Int J Plant Sci 155:828–836.

LePage BA, RS Currah, RA Stockey, GW Rothwell 1997 Fossil ectomycorrhizae from the Middle Eocene. Am J Bot 84:410–412.

Little SA, RA Stockey 2002 Fossil *Duabanga*-like leaves (Lythraceae) from the Princeton chert. Botany 2002 Abstracts, Botanical Society of America:59–60.

Mal TK, J Lovett-Doust, L Lovett-Doust 1997 Time-dependent competitive displacement of *Typha angustifolia* by *Lythrum salicaria*. Oikos 79:26–33.

Manchester SR, DL Dilcher, SLWing 1998 Attached leaves and fruits of myrtaceous affinity from the Middle Eocene of Colorado. Rev Palaeobot Palynol 102:153–163.

Matsumoto M, A Momohara, T Asakawa Ohsawa, Y Shoya 1997 Permineralized *Decodon* (Lythraceae) seeds from the Middle Miocene of Hokkaido, Japan, with reference to the biogeographic history of the genus. Jpn J Hist Bot 5:53–65.

Pigg KB, RA Stockey 1996 The significance of the Princeton chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. Wash Geol 24:32–36.

Pigg KB, RA Stockey, SL Maxwell 1993 *Paleomyrtinaea*: a new genus of permineralized myrtaceous fruits and seeds from the Eocene of British Columbia and Paleocene of North Dakota. Can J Bot 71:1–9.

Reid EM, MEJ Chandler 1933 The London Clay flora. British Museum (Natural History), London. 561 pp.

Robison CR, CP Person 1973 A silicified semiaquatic dicotyledon from the Eocene Allenby Formation of British Columbia. Can J Bot 51:1373–1377.

Rodríguez-de la Rosa, RA, SRS Cevallos-Ferriz, and A Silva-Pineda. 1998 Paleobiological implications of Campanian coprolites. Palaeogeogr, Palaeocl 142: 231–254.

Rouse GE, SK Srivastava 1970 Detailed morphology, taxonomy and distribution of *Pistillipollenites macgregori*. Can J Bot 48:287–292.

Russell LS 1935 A Middle Eocene mammal from British Columbia. Am J Sci 29:54–55.

Schenk H 1889 Ueber das Aërenchym, ein dem Kork homologes Gewebe bei Sumpfpflanzen. Jahrb Wiss Bot 20:526–74.

Schmid R 1980 Comparative anatomy and morphology of *Psiloxylon* and *Heteropyxis*, and subfamilial and classification of Myrtaceae. Taxon 29:559–595.

Schrenk J 1889 On the floating tissue of *Nesaea verticillata* (L.) H.B.K. Bull Torrey Bot Club 16:315–323, pls 95–97.

Sculthorpe CD 1967 The biology of aquatic vascular plants. Edward Arnold, London. 610 pp.

Shi S, Y Huang, F Tan, X He, DE Boufford 2000 Phylogenetic analysis of the Sonneratiaceae and its relationship to Lythraceae based on ITS sequences of nrDNA. J Plant Res 113:253–258

Stevens KJ, RL Peterson, GR Stephenson 1997 Morphological and anatomical responses of *Lythrum salicaria* L. (purple loosestrife) to an imposed water gradient. Int J Plant Sci 158:172–183.

Stockey RA 1983 *Pinus driftwoodensis* sp. nov. from the early Tertiary of British Columbia. Bot Gaz 144:148–156.

Stockey RA, WC Wehr 1996 Flowering plants in and around Eocene lakes of the interior. Pages 234–247 *in* R Ludvigsen, ed. Life in stone: a natural history of British Columbia's fossils. University of British Columbia Press, Vancouver.

Tiffney BH 1981 Fruits and seeds of the Brandon Lignite. VI. *Microdiptera* (Lythraceae). J Arnold Arbor Harv Univ 62:487–513.

Van Vliet GJCM 1978 Vestured pits of Combretaceae and allied families. Acta Bot Neerl 27:273–285.

Van Vliet GJCM, P Baas 1984 Wood anatomy and classification of the Myrtales. Ann Mo Bot Gard 71:783–800.

Wehr WC, DQ Hopkins 1994 The Eocene orchards and gardens of Republic, Washington. Wash Geol 22:27–34.

Wilson MVH 1977 Middle Eocene freshwater fishes from British Columbia. R Ont Mus Life Sci Contrib 113:1–61.

——— 1982 A new species of *Amia* from the Middle Eocene of British Columbia. Palaeontology 25:413–424.

Wolfe JA, T Tanai 1980 The Miocene Seldovia Point flora of the Kenai Group, Alaska. U S Geol Surv Prof Pap 1105:1–52.

**Fig. 2.1** *Decodon allenbyensis* rooting systems. *a*, Peel with transverse and oblique sections of branching roots producing thin-walled lacunate phellem. P5105 D bot #1a, ×3.2. *b*, Transverse and longitudinal section of branching roots surrounded by thin-walled lacunate phellem. P5956 E bot #1b, ×4.1. *c*, Transverse section of submerged bent stem giving rise to adventitious roots. P6427 L top #1, ×1.2. *d*, Transverse section of root showing phloem fiber bundles and positions of numerous dark bands of small rectangular cells in lacunate phellem. P6019B #6, ×3.6.

**Fig 2.1**

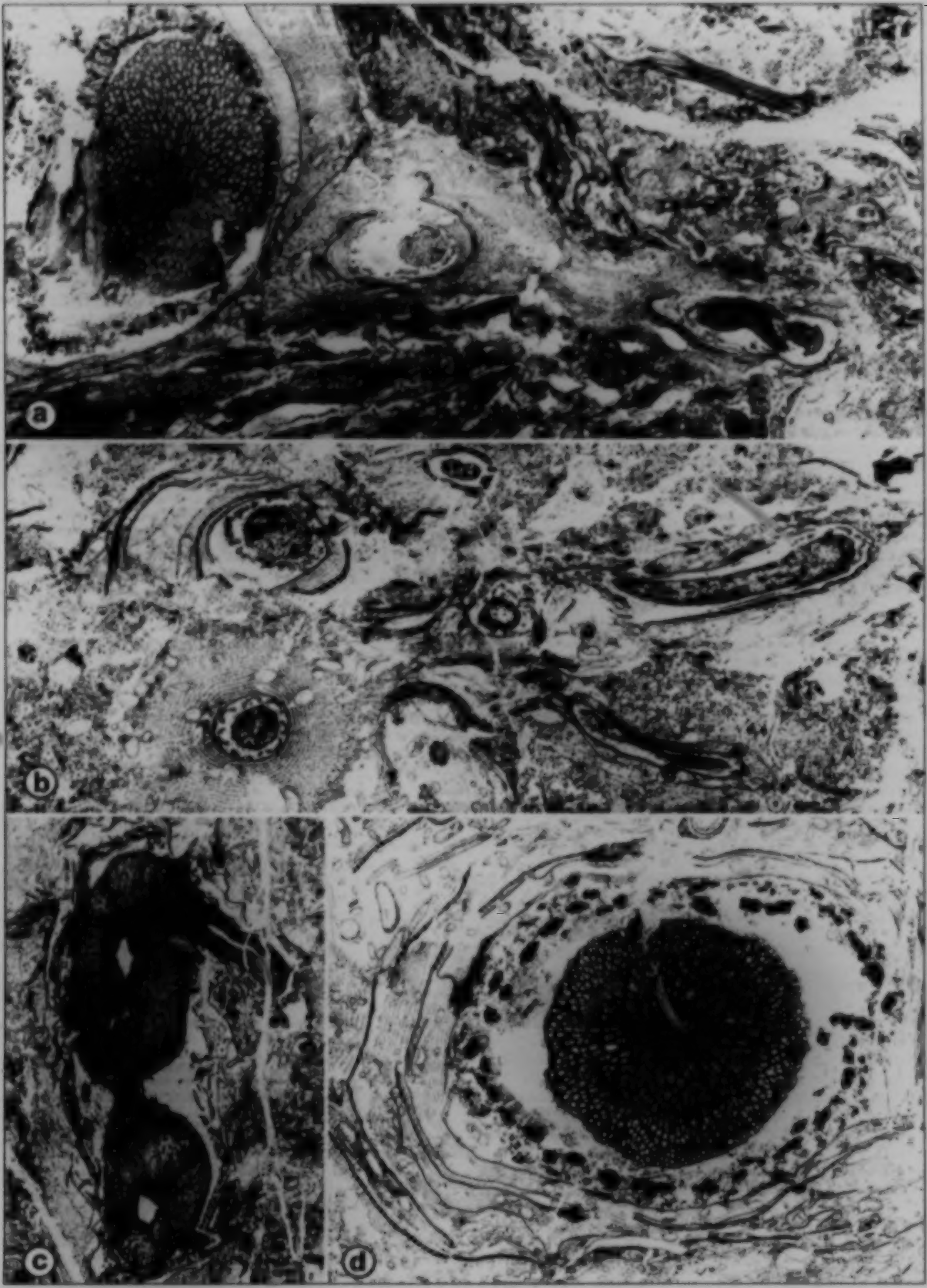


**Fig. 2.2** *Decodon allenbyensis* and *Decodon verticillatus* stems and roots. *a*, Longitudinal section of a large degraded *D. allenbyensis* stem (at top) with branching adventitious roots. Arrows indicate young roots. P6427 L bot #6, ×0.7. *b*, *D. verticillatus* stem with adventitious roots. ×0.9. *c*, *D. allenbyensis* root, transverse section showing numerous bands of phellem. P5912 H top #1, ×14. *d*, *D. allenbyensis* root stele showing diffuse porous wood with large-celled rays. Arrows indicate phloem fiber bundles. P5912 H top #1, ×4.6. *e*, *D. allenbyensis* young roots in transverse section showing elongate hypodermal cells, aerenchymatous cortex, and pentarch stele at right. P6427 K bot #34, ×72. *f*, *D. allenbyensis* hexarch root stele. P6427 K bot #56, ×37. *g*, *D. allenbyensis* very small young root. P5956 E bot #1b, ×122.

Fig. 2.2

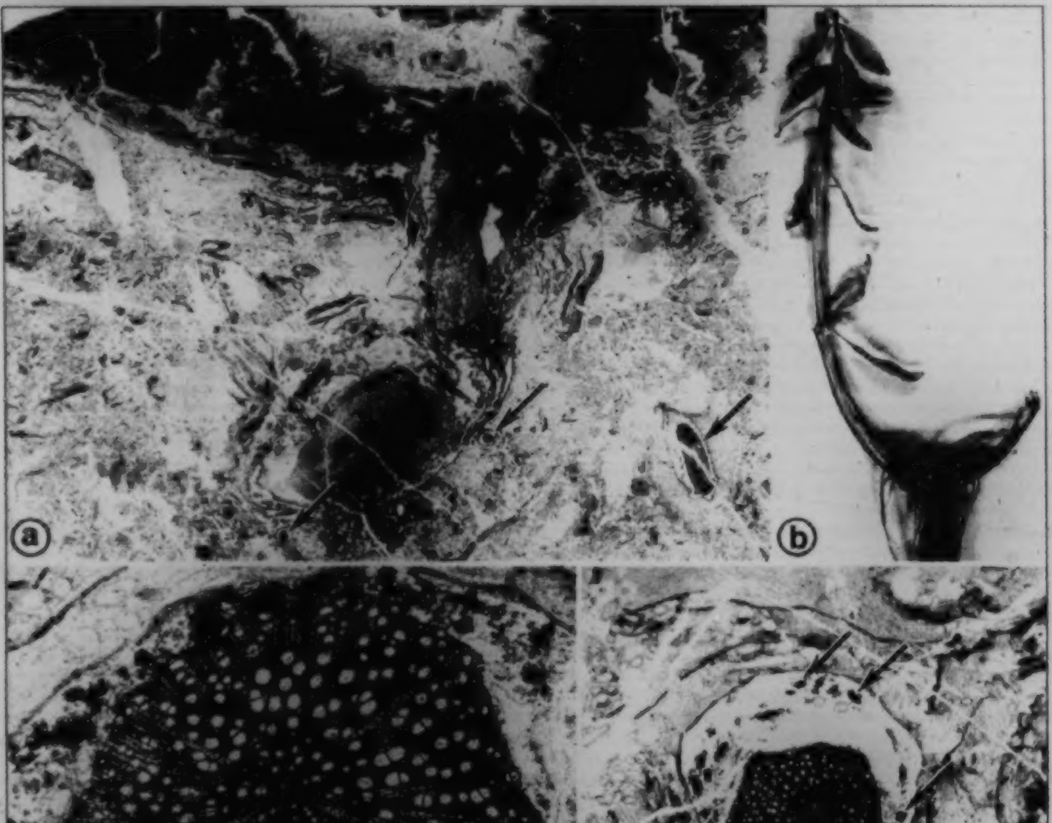


**Fig. 2.3** Fossil *Decodon allenbyensis* roots. *a*, Transverse section of young branching root showing cortex with fungal chlamydospore-like structures and radially elongate hypodermal cells. P5956E bot #1b, ×48. *b*, Transverse section of young root cortex showing numerous fungal hyphae and possible chlamydospores. P5956 E bot #1b, ×110. *c*, Transverse section of phloem showing fiber bundles and periderm, at top. P6427 L bot #6, ×21. *d*, Root wood, transverse section showing solitary vessels in radial multiples and rays with large cells. P6019 B #6, ×23. *e*, Root wood, radial longitudinal section showing heterogeneous rays with both upright and procumbent cells. P6288A #3, ×35. *f*, Root wood, tangential section showing tall rays. P6427 L bot #11, ×32. *g*, Root wood, tangential section showing five-seriate ray, center. P1303 C1 side #2, ×23. *h*, Root wood, tangential section showing septate fiber (arrow). P6427 L bot #11, ×73. *i*, Vessel elements with simple perforations. P4947 A #12, ×255. *j*, Vessel element showing crowded alternate pitting. P6427 L bot #11, ×225. *k*, Root wood, radial section showing vessel elements with possible tyloses. P6288 A #3, ×53.

Fig. 2.3

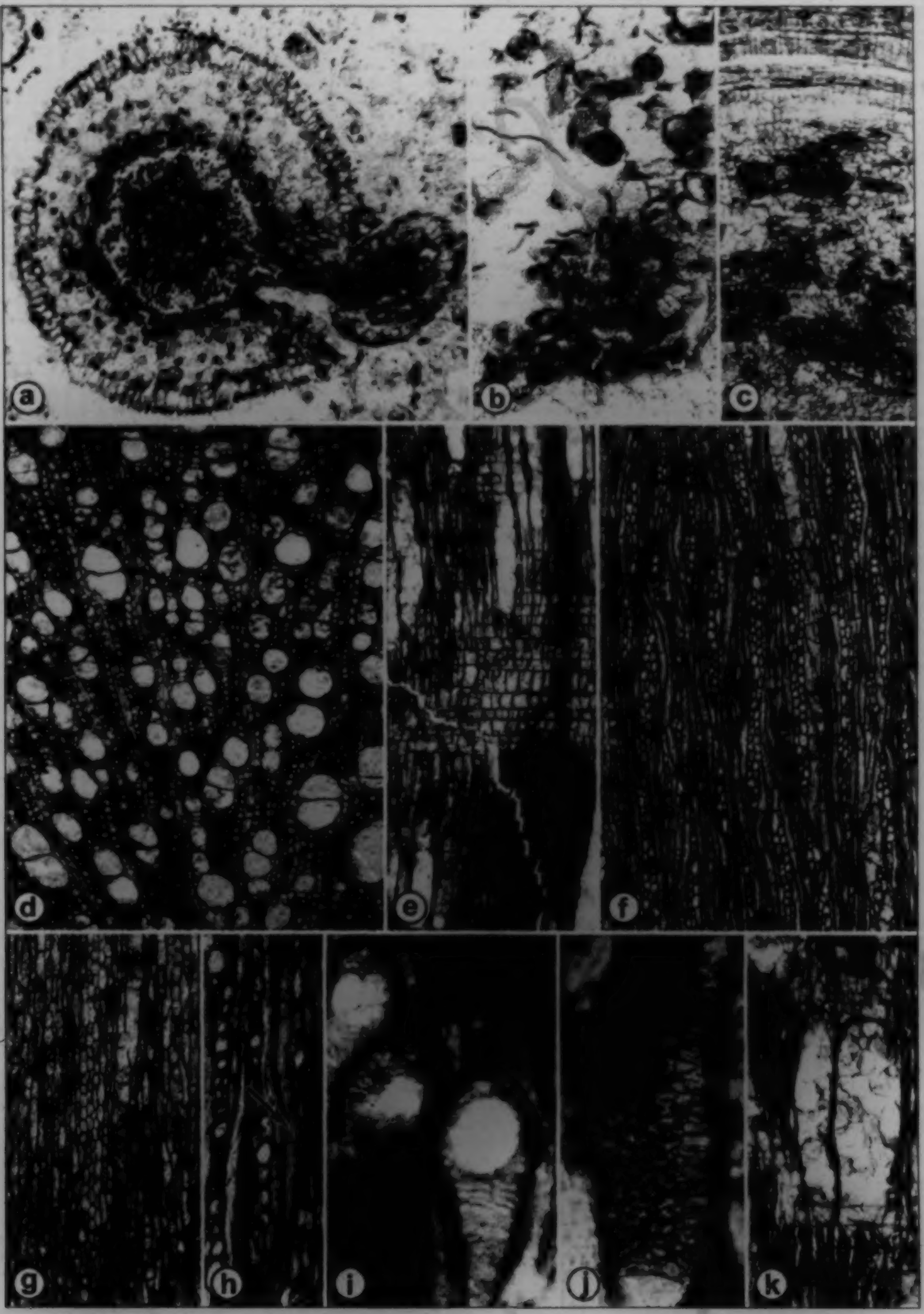


**Fig. 2.4** *Decodon allenbyensis* (fossil) and *Decodon verticillatus* (extant) roots under SEM. *a*, *D. allenbyensis*, showing elongate-bordered pits with slit-like apertures and vestures. P1303 $C_1$ side #8, ×2148. *b*, *D. allenbyensis* enlarged vessel element pit cavity showing type B vesturing. P1303 $C_1$ side #8, ×4443. *c*, *D. verticillatus* transverse section of young root showing stele, aerenchymatous cortex, and radially elongate hypodermal cells; freeze fractured in cryo-SEM. Decrt00, ×23. *d*, Fossil vessel element wall showing mold-casts of alternate pits with type B vestures. P1303 $C_1$ side #8, ×3029. *e*, Transverse section of young extant *Decodon* root with hexarch stele and endodermis; freeze fractured in cryo-SEM. Decrt06, ×149. *f*, Longitudinal section of extant *Decodon* root wood, showing vessel element with scalariform perforation plate and alternate pitting. Decrtl01 stub#2, ×275. *g*, Longitudinal section of root wood, showing vessel element with simple perforation plate and alternate pitting. Decrtl05 stub#3, ×638. *h*, Transverse section of aerenchymatous primary cortex in young root of extant *Decodon*; freeze fractured in cryo-SEM. Decrt02, ×168.

Fig 2.4

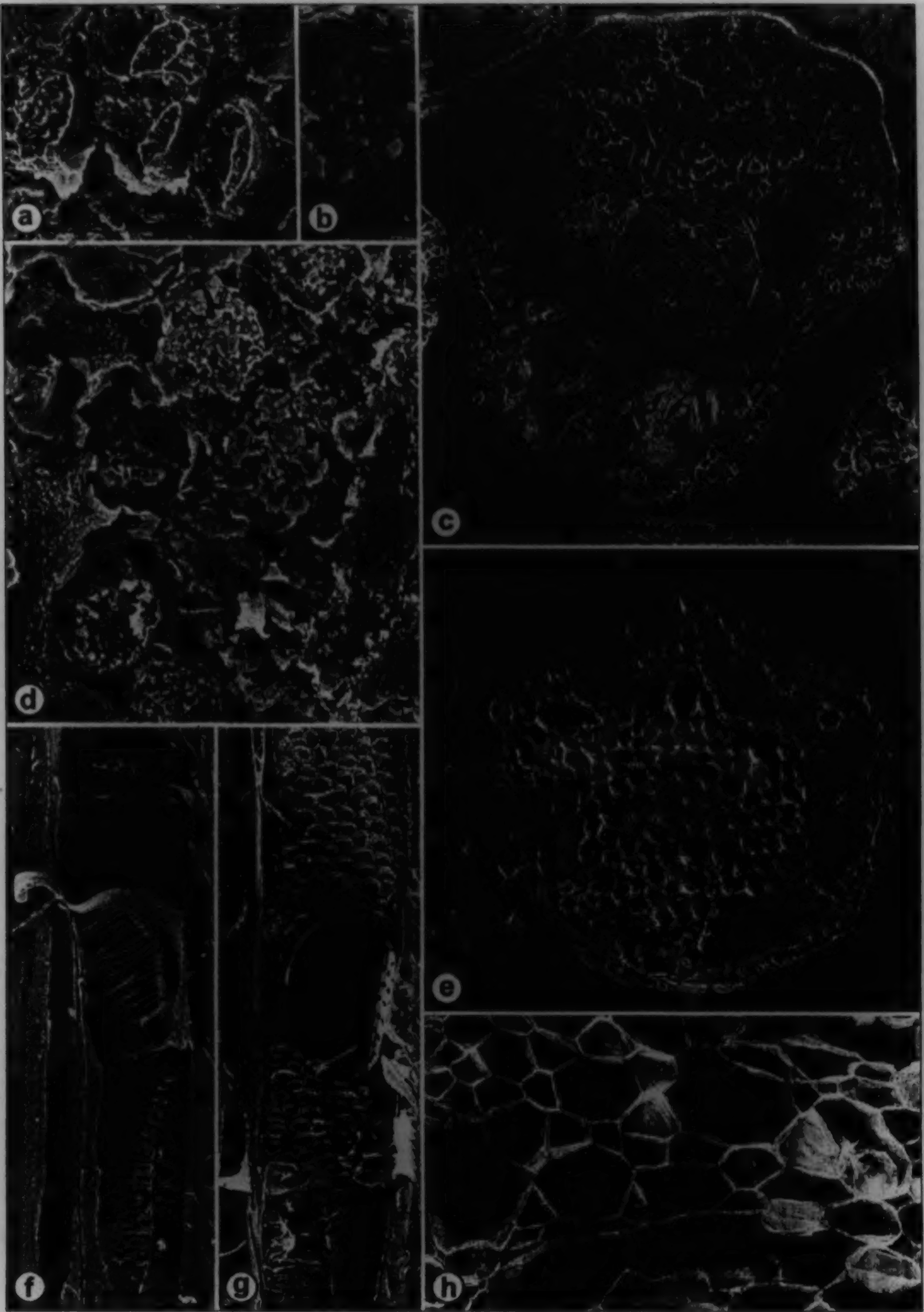


**Fig. 2.5** *Decodon verticillatus* root wood anatomy. *a*, Transverse section showing diffuse porous wood and rays with large cells. SL12720, ×12. *b*, Radial longitudinal section showing heterocellular rays with upright and procumbent cells. SL12721, ×52. *c*, Tangential longitudinal section showing unicellular and multicellular rays. SL12722 ×25.

Fig. 2.5

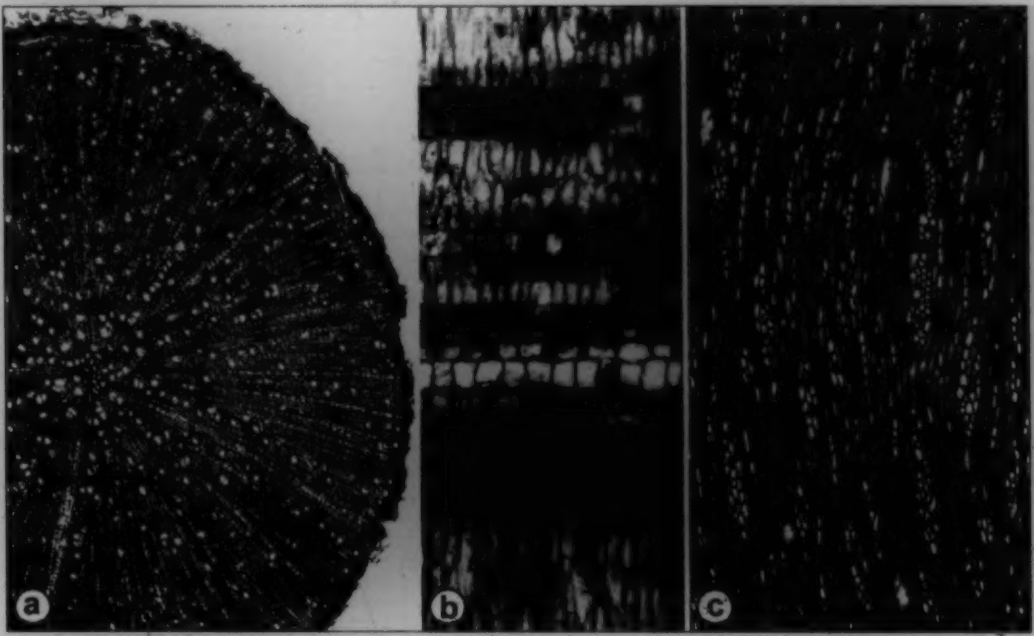


**Fig. 2.6** Phellem of fossil and extant *Decodon*. *a*, *Decodon allenbyensis* thin-walled lacunate phellem. P6288 A #3, ×25. *b*, Transverse section of *D. allenbyensis* phellem showing regular pattern of lacunae. P6288 A #3, ×73. *c*, Phellem of *D. allenbyensis* showing radially elongated T-shaped cells and unelongated cells with dark contents (bottom). P6288 A #3, ×105. *d*, Lacunate phellem of *D. allenbyensis* showing unelongated rectangular cells (arrows). P5105 D bot #2, ×39. *e*, *Decodon verticillatus* lacunate phellem under critical-point drying and SEM. Decphl01 stub#6, ×47. *f*, *D. verticillatus* phellem showing branched, T-shaped cells and lacunae under critical-point drying and SEM. Decphl02 stub#6, ×62.

Fig. 2.6

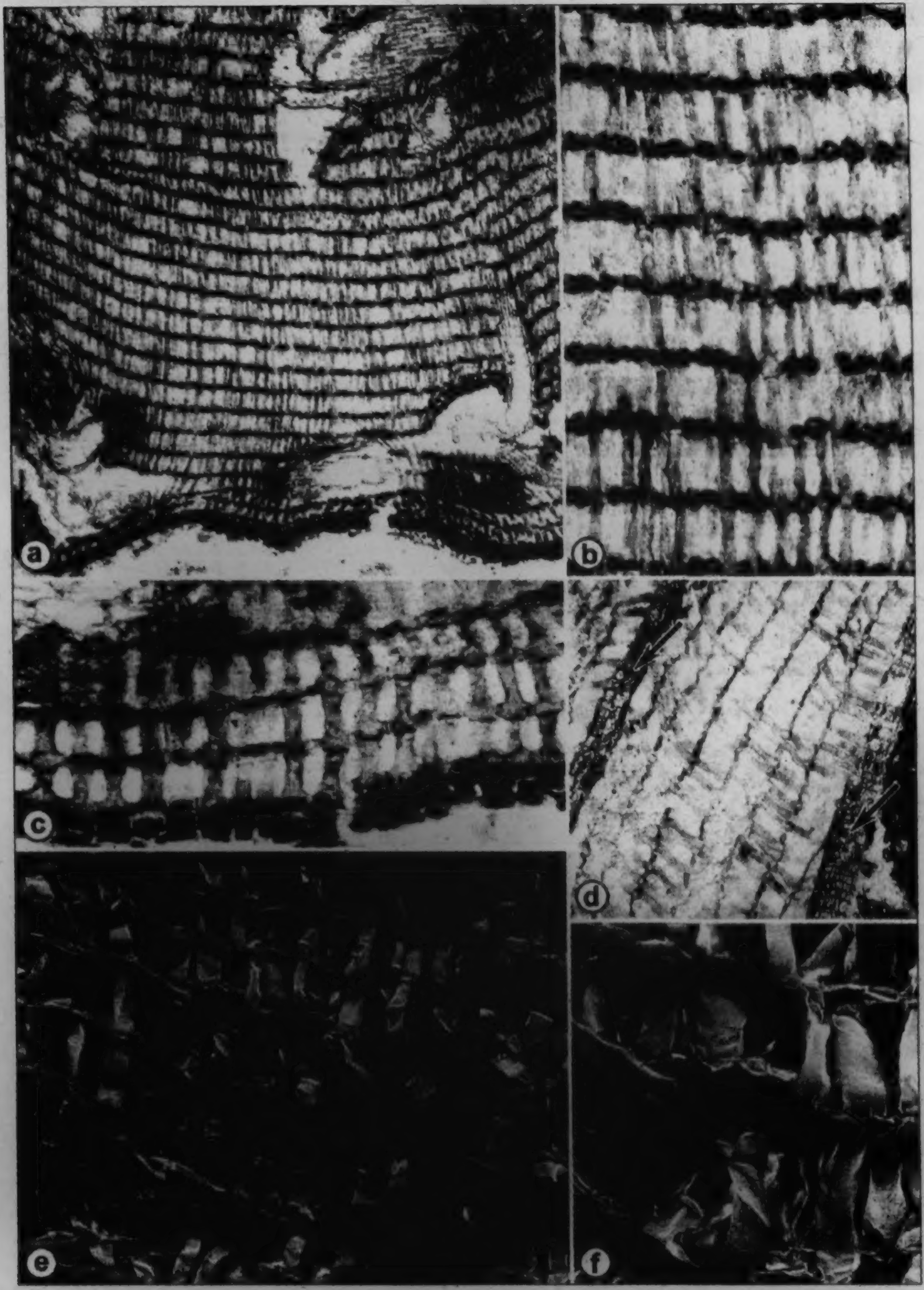


**Fig. 2.7** Extant and fossil *Decodon* stems. *a*, Transverse section of young *Decodon allenbyensis* stem with well-preserved cortical tissues. P6394 G bot #0, ×6. *b*, Transverse section through *Decodon verticillatus* secondary phloem and periderm, showing phloem fiber bundles (arrows). SL12725, ×32. *c*, Transverse section of *D. verticillatus* young branching stem. SL12726, ×15. *d*, Transverse section of decorticated stem of *D. allenbyensis* showing pith and diffuse porous wood. P5949 B bot #1a, ×7. *e*, Transverse section of *D. allenbyensis* wood with three growth increments showing vessels solitary and in radial multiples. P1982 D bot #1b, ×49. *f*, Radial longitudinal section of *D. verticillatus* wood, showing upright and procumbent cells of heterocellular ray. SL12729, ×25. *g*, Tangential longitudinal section of *D. allenbyensis* wood showing both narrow and wide, often tall, rays. P6427 K bot #56, ×22. *h*, Radial longitudinal section of *D. allenbyensis* wood showing upright, weakly procumbent, and procumbent cells of heterocellular ray. P6427 K bot #24, ×39. *i*, Tranverse section of *D. allenbyensis* phloem. Arrows indicate fiber bundles. P6427 K bot #57, ×29. *j*, Tangential longitudinal section of *D. verticillatus* wood showing narrow and wide, often tall, rays. SL12732, ×29. *k*, *D. verticillatus* vessel elements with simple perforations. SL12733, ×147.

**Fig. 2.7**

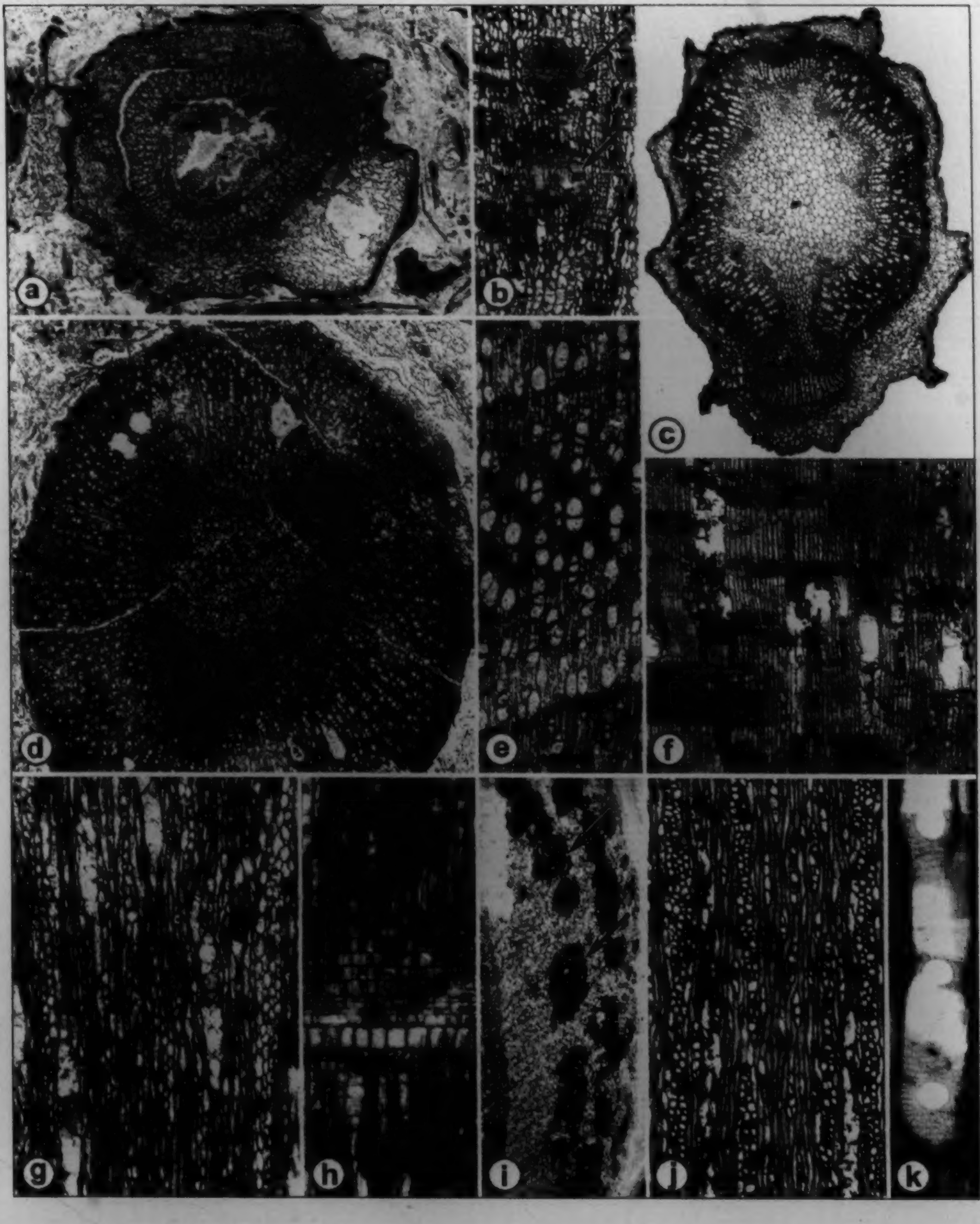
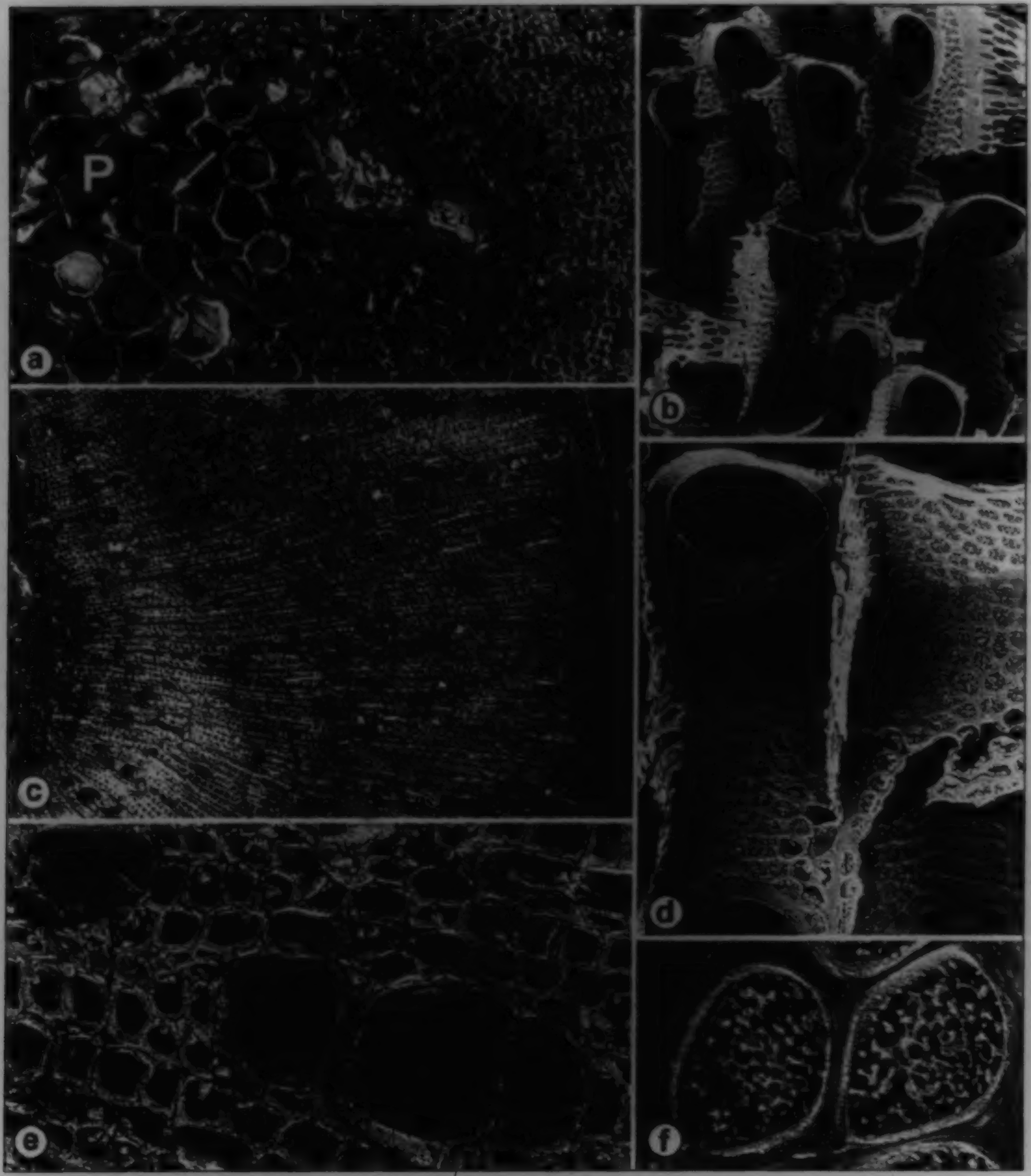


**Fig. 2.8** *Decodon verticillatus* stem wood under SEM. *a*, Transverse section showing pith (*P*) and wood. Arrow indicates druse. Decxs04 stub#1, ×41. *b*, Tangential longitudinal section showing vessel elements with simple perforations. Decod22 stub#10, ×193. *c*, Transverse section with vessels solitary and in radial multiples. Decxs01 stub#1, ×32. *d*, Tangential longitudinal section showing vessel elements with alternate vestured pitting and simple perforations. Decod21 stub#11, ×396. *e*, Transverse section showing oval starch grains in fibers, single vessel element (upper left), and radial multiple of four. Decxs02 stub#1, ×248. *f*, Tangential longitudinal section of wood showing type B vestured pits. Decod17 stub#11, ×3335.

Fig. 2.8



# CHAPTER 3

## Morphogenesis of the specialized peridermal tissues in *Decodon allenbyensis*[1]

### INTRODUCTION

The term 'aerenchyma' was originally coined by Schenck (1889) to describe lacunate tissue derived from a phellogen (Ellmore 1981). Such tissues, also called lacunate phellem (Lempe *et al.* 2001), are found in numerous aquatic and semi-aquatic plants (Schenck 1889; Sculthorpe 1967). Lacunate phellem occurs in several semi-aquatic taxa in Lythraceae, Melastomataceae, Onagraceae, Euphorbiaceae (Schenck 1889), Myrtaceae (Cook *et al.* 1980), and Fabaceae (Schenck 1889; Shimamura *et al.* 2002, 2003), and is thought to be an adaptation for aeration of submerged axes. Recent work by Stevens *et al.* (2002) on *Lythrum salicaria* L. (Lythraceae) has established the first direct evidence for gaseous connection between shoots and submerged roots via lacunate phellem.

Lythraceae, an angiosperm family of 31 genera and 600 species (Graham 1964; Graham *et al.* 1993; Judd *et al.* 1999) has several taxa with lacunate phellem. *Decodon verticillatus* (L.) Ell. is known to produce abundant lacunate phellem in submerged conditions (Schrenk 1889; Graham 1964; Lempe *et al.* 2001). Recently the anatomically preserved aquatic roots and stems of the fossil plant *Decodon allenbyensis* Cevallos-Ferriz *et* Stockey 1988, were described, and well-preserved aerenchymatous tissues were shown (Little & Stockey 2003). This study describes, in detail, the development of aquatic tissues in submerged axes of *Decodon allenbyensis*. Transitions from primary tissue organization to the development of secondary tissues are illustrated and a novel rhytidome system is described.

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[1] A version of this chapter has been published. Little and Stockey 2006. International Association of Wood Anatomists Journal 27: 73-87.

## MATERIALS AND METHODS

Permineralized *Decodon* axes come from the Princeton Chert (Allenby Formation), located on the east bank of the Similkameen River approximately 8.4 km southwest of the town of Princeton, British Columbia (UTM 783724; 49° 22.7' N, 120° 32.7' W). The locality is dated as Middle Eocene, based on data from pollen (Rouse & Srivastava 1970), fossil mammals (Russell 1935; Gazin 1953), fish (Wilson 1977, 1982), and potassium-argon dating (Hills & Baadsgaard 1967; H. Baadsgaard, pers. commun. 1999).

Chert slabs were prepared using the cellulose acetate peel technique (Joy *et al.* 1956) modified for hydrofluoric acid (Basinger & Rothwell 1977; Basinger 1981). Specimens (SL12708–SL123104) are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA). Peel sections were mounted with Eukitt rapid mounting medium (O. Kindler GmbH & Co., Freiburg, Germany) for microscopic examination. Images were taken with a Microlumina (Leaf Systems, Inc.) digital scanning camera and a Phase One digital studio camera (Phase One A/S, Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe Photoshop.

## RESULTS

Numerous interconnected branching roots of *Decodon allenbyensis* were described by Little and Stockey (2003). Roots arise adventitiously from stems, and many of these have tissues typical of aquatic plants. Stems and roots without aerenchymatous tissues also occur in the chert, but most of the remains have either an aerenchymatous primary cortex or lacunate phellem. Further observations on the development of the tissues in aquatic axes are described below.

### *Primary growth*

Abundant small roots lacking secondary tissues are found both isolated in the chert matrix and attached to larger woody axes (Fig. 3.1a–d). Exarch actinosteles are surrounded by an endodermis that is composed of dark, rectangular cells (Fig. 3.1a–d). In many young roots there are several layers of inner cortical cells adjacent to the endodermis that also have dark contents (Fig. 3.1a–d). Primary phloem and pericycle are present but are not usually well preserved. Primary xylem is pentarch to hexarch (Fig. 3.1b, c) and rarely septarch (Fig. 3.1d). Primary phloem lacks sclereids or phloem fiber bundles at this stage of development (Fig. 3.1a–d).

Primary cortex of young roots is typically aerenchymatous (Fig. 3.1a, b) but does not always appear so in the youngest roots (Fig. 3.1a, double arrow). Beneath the epidermis is a distinctive hypodermis one cell layer thick, composed of radially elongate cells with internally thickened walls (Fig. 3.1a, b; e left inset). Epidermal cells are rectangular in transverse section and are much smaller than the hypodermal cells (Fig. 3.1a, b).

### *Transition to secondary growth*

Early stages of development (shortly after initiation of secondary growth) are preserved in the Princeton Chert specimens and provide information on the timing and synchronization of wood and periderm production in this fossil plant. Initiation of the vascular cambium, and subsequent secondary xylem and phloem production, precedes the initiation of phellogen activity. Evidence for this timing of cambial activity is shown by roots that possess small amounts of wood and secondary phloem but no periderm (Fig. 3.1a). These roots still have intact epidermis with an aerenchymatous primary cortex surrounding a partially woody stele (Fig. 3.1a).

Phellogen initiation occurs in the pericycle. In aquatic roots the phellogen produces a lacunate phellem. This is in contrast to non-aquatic roots that produce radially aligned compact rectangular phellem. At the time of phellogen formation the secondary phloem begins to produce clusters of fiber bundles (Fig. 3.1e, at arrows), while in both the primary and early secondary phloem there are no phloem fiber bundles (Fig. 3.1b, c). The primary cortex is sloughed off by the early lacunate phellem and in relatively young specimens the delicate aerenchymatous primary cortex is still associated with the root (Fig. 3.1e).

### *Secondary growth*

*Xylem* – Wood with distinct growth increments (Fig. 3.3) and secondary phloem are produced in older axes (Fig. 3.2, 3.3). These larger roots are easily distinguished from other root types in the matrix by their diffuse and wide vessels, large parenchymatous ray cells and lacunate phellem. Wood anatomy of the fossil roots and stems have been described in detail in chapter 2.

*Phloem* – Secondary phloem is composed of thin-walled cells and clusters of phloem fiber bundles (Fig. 3.1e, 3.2, 3.3, 3.5a). Even when phloem cells are largely missing due to poor preservation, the thick-walled fibers are prominent (Fig. 3.1e, 3.2a, 3.3). Fiber bundles typically range 156–700 μm in diameter. Individual fibers are round to polygonal in transverse section, 39–147 μm in diameter.

*Phellem* – Aquatic lacunate phellem, a very delicate tissue that is difficult to study in living plants (Lempe *et al.* 2001; Stevens *et al.* 1997, 2002; Little & Stockey 2003), is usually well preserved and intact in the Princeton fossils (Fig. 3.1e, 3.2a, 3.3, 3.4). The expanded aerenchymatous lacunate phellem appreciably widens the diameter of young roots that have very little secondary vascular tissue. Such young roots typically measure 0.5 mm to 15 mm in diameter (Fig. 3.2a, 3.3b).

At low magnifications phellem appears highly organized with ordered concentric layers of cells surrounding the vascular cylinder (Fig. 3.2a, 3.3). At regular intervals bands ca. 3 to 5 cells thick, of dark-colored rectangular ‘phelloids’ (‘phellem-like cells’ *sensu* Esau 1965) (Fig. 3.4a, c), occur among the light colored thin-walled lacunate phellem (Fig. 3.3). Up to 12 such rings of phelloids are present in some roots. The light colored, thin-walled lacunate phellem is composed of T-shaped cells, with radial extensions and air spaces between cells (Fig. 3.4).

*Rhytidome* – The largest axes of *Decodon allenbyensis*, some with up to 18 growth increments of wood, have a complex rhytidome with tissue organization that is distinct from that of the lacunate phellem system described above (Fig. 3.5c). The rhytidome is composed of alternating bands of non-aquatic periderm and aerenchymatous secondary phloem (Fig. 3.5c, 3.7). Phloem bands have typical phloem fiber bundles (Fig. 3.5b, c). The periderm bands vary in thickness, from 5–25 cells thick per band, or rarely up to ~50 cells thick per band.

Parenchymatous cells in the phloem have tangentially aligned extensions with air spaces between cells. Rectangular cells, lacking extensions, are arranged in radial rows between the elongate cells with lacunae (Fig. 3.5b, d). Rhytidome with up to five bands of 'lacunate phloem' have been observed around an axis. However, this aerenchymatous phloem is also commonly found as isolated fragments that have been sloughed off the plants and preserved in the chert matrix.

While most roots have lacunae in the non-active secondary phloem there is rare non-lacunate phloem with transitions from non-lacunate phloem to lacunate phloem also observed. Throughout the rhytidome the zones of periderm are composed of radially aligned compact phelloids. These periderm bands maintain their organization and structure and do not radially elongate to produce lacunae.

## DISCUSSION

The present investigation provides additional developmental data on aquatic tissues in the submerged axes of the fossil aquatic dicot, *Decodon allenbyensis*, originally known only from isolated fruits and seeds (Cevallos-Ferriz & Stockey 1988). Recent studies on this species from the Princeton Chert have produced data on the growth habit, anatomy of roots and stems (Little & Stockey 2003), and anatomy of the leaves of this plant (Little & Stockey 2002; Little et al. 2004; chapter 4). The present study adds to knowledge of the growth and morphogenesis of peridermal tissues in this plant, making *D. allenbyensis* the best known fossil *Decodon* species.

In the fossilized roots of *Decodon allenbyensis*, the morphogenesis of aquatic tissues follows a consistent sequence. Primary cortex in roots forms lacunae beneath intact dermal layers prior to secondary vascular cambium initiation. The vascular cambium is the first to produce secondary tissues. Shortly after vascular cambial activity is initiated, fiber bundles develop in the secondary phloem and are present in all later produced secondary phloem. Phellogen activity is then initiated in the pericycle. Lacunate phellem is produced by the phellogen in submerged conditions. Lacunae in the phellem were most likely formed by the radial elongation of phellem cells as in extant *D. verticillatus* (Schrenk 1889; Lempe *et al.* 2001).

The anatomy of primary and secondary aquatic tissues in the fossil roots is comparable with those of living *Decodon verticillatus* roots (Little & Stockey 2003). The coordination of the timing of secondary tissue initiation in roots of extant *D. verticillatus* is also identical to that in the fossil roots. Primary cortex forms lacunae beneath intact dermal layers, followed by secondary vascular cambium growth with phloem fiber bundles (Little & Stockey 2003). In the pericycle, phellogen activity is initiated as is typical in Lythraceae (Graham 1964; Lempe *et al.* 2001), and in aquatic conditions phellem undergoes radial elongation to produce T-shaped cells with air spaces between (Schrenk 1889; Lempe *et al.* 2001). These early stages in the development of primary and secondary aquatic modifications in roots of living *D. verticillatus* are similar in all respects to those in the fossil roots.

Members of Onagraceae produce a tissue in young roots that is strikingly similar in appearance to lacunate phellem, but it is a primary tissue (Schenck 1889; Ellmore 1981; Fig. 3.6A). As cortical parenchyma radially elongates to form regular and rectangular lacunae, the outer cortical parenchyma is disrupted and the epidermis is torn (Schenck 1889; Ellmore 1981). Ellmore (1981) corroborated Schenck's (1889) original developmental interpretation of this tissue in species of *Ludwigia* and clearly showed that the phellem-like aerenchyma, in aerial roots of *Ludwigia peploides* (Onagraceae), is a primary tissue (Fig. 3.6A).

In contrast to this '*Ludwigia*-type' of primary cortical aerenchyma development, roots of extant *Decodon* and of the fossil described here have '*Decodon*-type' development with more circular lacunae that form beneath intact dermal layers (Fig. 3.6B). Although lacunate phellem and *Ludwigia*-type primary aerenchyma have different developmental origins, their superficial resemblance has lead to misidentification (Metcalfe & Chalk 1950, 1983; Sculthorpe 1967). Without the observation of the early stages of morphogenesis in the fossil roots with lacunate phellem it would be difficult to distinguish which type of aerenchyma development is present. However, the excellent *in situ* preservation and the wide range of morphogenetic stages of these plants provide the information necessary to illustrate the *Decodon*-type primary aerenchyma development in the fossil roots of *D. allenbyensis* and to demonstrate morphogenetic similarities to extant *D. verticillatus* (Little & Stockey 2003).

The bands of compact phelloids with suberized walls that occur in the phellem of extant *Decodon verticillatus* (Schrenk 1889) and in the fossil *Decodon allenbyensis* were hypothesized to be evidence of consecutive phellogen production (Little & Stockey 2003). Similar bands of compact suberized cells are also seen in the lacunate phellem of submerged axes in extant species of *Leptospermum* J.R. Forst. & G. Forst., and these bands have also been interpreted as evidence for consecutive phellogen production (Cook *et al.* 1980). Schrenk (1889) states that the suberized bands are tightly sealed, preventing gas exchange between the inner part of an axis and the majority of the aerenchyma to the outside of this layer. Since lacunate phellem is produced more abundantly below the axes than above in a horizontal axis, and because the bands of phelloids are sealed by suberin, Schrenk (1889) concluded that in *Decodon verticillatus* lacunate phellem must only serve to aid in buoyancy. However, lacunate phellem in living and fossil *Decodon* species probably does aid aeration, an idea supported by recent work on *Lythrum salicaria* by Stevens *et al.* (2002), which demonstrates a gaseous connection between submerged and non-submerged axes. In addition to gaseous exchange the phellem probably also serves in flotation since it is produced in such large amounts in both the living and fossil taxa.

Lacunate phellem is the most prevalent form of periderm in the fossil axes. In living *D. verticillatus* the radially elongate cells of the lacunate phellem have cellulose walls and the bands of compact phelloids have suberized walls (Schrenk 1889). The fossil lacunate phellem probably also had walls with similar components to those of living *Decodon*. However, trying to draw additional parallels between the fossil periderm and the periderm of other extant taxa may not be advisable since aquatic phellem develops differently in members of Lythraceae (Lempe *et al.* 2001), and aquatic phellem is also found in various unrelated groups (Schenck 1889; Cook *et al.* 1980; Shimamura *et al.* 2002, 2003). Further studies on lacunate phellem in Lythraceae and other families are needed in order to assess variation in details of anatomy and composition, as well as the various potential developmental syndromes in these plants.

The largest fossil axes observed, with several woody growth increments, have a rhytidome with more complex tissue organization than that seen in the smaller axes with lacunate phellem (Fig. 3.7). Consecutive phellogens are formed as in lacunate phellem discussed above, but bands of non-elongate phelloids are produced and the number of cells per layer is larger than three per band typically found in the lacunate phellem. These thick bands of phelloids were probably suberized and waterproof, similar to suberized bands in lacunate phellem of extant *Decodon*. The bands of phloem with lacunae and fiber bundles are found between the compact phelloid bands and were presumably non-active. This 'lacunate phloem' probably replaced the lacunate phellem in the function of aeration and/or flotation. Tangential elongation of cells in the non-active phloem contrasts with the radial elongation of cells in lacunate phellem of smaller axes. Parenchyma is the most likely cell type to be tangentially elongated in the non-active phloem. This lacuna production probably would have occurred just prior to, or just after the phloem was cut off by a new phellogen. Tangential elongation in lacunate phloem of the rhytidome would better accommodate increases in girth of the large woody axes than the radially elongate cells of lacunate phellem. The alternating rings of phelloids, several cells thick, would have provided more protection from mechanical damage and microbial attack than thin-walled lacunate phellem. However, this rhytidome system was probably shed regularly because it is commonly found isolated in the chert suggesting that its main function was to accommodate increases in girth due to woody growth of the axes.

Little and Stockey (2003) hypothesized that the fossil, *Decodon allenbyensis*, was larger than the extant species *Decodon verticillatus*. The representative size of stems from lake populations in Ohio ranges from 2–4 cm in diameter including some roots (Shirley A. Graham, pers. commun. 2002). Plants in the southernmost populations, such as those in Florida, may get as wide as the largest fossil axes (~20 cm in diameter) (Christopher G. Eckert, pers. commun. 2001), but no girth measurements have yet been documented. Further investigations are required to determine whether extant *Decodon* can reach the size of the fossil species. Such investigations may determine whether the complex aquatic rhytidome, seen here in the fossil, is also produced by large axes of extant *Decodon*. However, such delicate aerenchymatous tissue may prove harder to observe in life than in the permineralized tissues of the fossils without special techniques such as critical point drying or freeze fracturing (Lempe *et al.* 2001; Little & Stockey 2003).

The remains from the Princeton Chert have provided crucial comparative anatomy that is of systematic importance, and highlight the aquatic habitat at the time of preservation. Such detailed understanding of the anatomical structure and sequence of the various stages of primary and secondary aquatic anatomical adaptations for a fossil plant is rare. As a result of this study the anatomical and developmental data now known for *Decodon allenbyensis* is more complete than that of most extant Lythraceae. Currently, the aquatic rhytidome made up of alternating bands of compact phelloids and non-active secondary lacunate phloem is considered unique and has not been previously described in living or fossil plants.

## LITERATURE CITED

Basinger, J.F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. Can. J. Bot. 59: 2379–2410.

Basinger, J.F. & G.W. Rothwell. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. Can. J. Bot. 55: 1984–1990.

Cevallos-Ferriz, S.R.S. & R.A. Stockey. 1988. Permineralized fruits and seeds from the Princeton Chert (Middle Eocene) of British Columbia: Lythraceae. Can. J. Bot. 66: 303–312.

Cook, J.M., A.F. Mark & B.F. Hore. 1980. Responses of *Leptospermum scoparium* and *Leptospermum ericoides* (Myrtaceae) to waterlogging. New Zeal. J. Bot. 18:233–246.

Ellmore, G.S. 1981. Root dimorphism in *Ludwigia peploides* (Onagraceae): structure and gas content of mature roots. Amer. J. Bot. 68: 557–568.

Esau, K. 1965. Plant anatomy, Ed. 2. John Wiley & Sons, New York. 767 pp.

Gazin, C.L. 1953. The Tillodontia: an early Tertiary order of mammals. Smithson. Misc. Collect. 1221: 1–110.

Graham, S.A. 1964. The genera of Lythraceae in the southeastern United States. J. Arnold Arbor. 45: 235–251.

Graham, S.A., J.V. Crisci & P.C. Hoch. 1993. Cladistic analysis of the Lythraceae sensu lato based on morphological characters. Bot. J. Linn. Soc. 113: 1–33.

Hills, L.V. & H. Baadsgaard. 1967. Potassium-argon dating of some lower Tertiary strata in British Columbia. Bull. Can. Petrol. Geol. 15: 138–149.

Joy, K.W., A.J. Willis & W.S. Lacey. 1956. A rapid cellulose peel technique in palaeobotany. Ann. Bot. (London) n.s. 20: 635–637.

Judd, W.S., C.S. Campbell, E.A. Kellogg & P.F. Stevens. 1999. Plant systematics: a phylogenetic approach. Sinauer Associates, Inc. Sunderland MA. 423 pp.

Lempe, J., K.J. Stevens & R.L. Peterson. 2001. Shoot responses of six Lythraceae species to flooding. Plant Biol. 3 (2): 186–193.

Little, S.A. & R.A. Stockey. 2002. Fossil *Duabanga*-like leaves (Lythraceae) from the Princeton Chert. Annual Bot. Soc. of America meeting, Madison WI. Abstact: F–4.

Little, S.A. & R.A. Stockey. 2003. Vegetative growth of *Decodon allenbyensis* (Lythraceae) from the Middle Eocene Princeton Chert with anatomical comparisons to *Decodon verticillatus*. Int. J. Plant Sci. 164: 453–469.

Little, S.A., R.A. Stockey, & R. C. Keating. 2004. *Duabanga*-like leaves from the Middle Eocene Princeton Chert and comparative leaf histology of Lythraceae sensu lato. Amer. J. Bot. 91: 1126–1139.

Metcalfe, C.R. & L. Chalk. 1950. Anatomy of the Dicotyledons, vol. 2: 664–667. Oxford University Press, Oxford, UK.

Metcalfe, C.R. & L. Chalk. 1983. Anatomy of the Dicotyledons, Ed. 2, vol. 2: 134–136. Clarendon Press, Oxford, UK.

Rouse, G.E. & S.K. Srivastava. 1970. Detailed morphology, taxonomy and distribution of *Pistillipollenites macgregori*. Can. J. Bot. 48: 287–292.

Russell, L.S. 1935. A Middle Eocene mammal from British Columbia. Amer. J. Sci. 29: 54–55.

Schenck, H. 1889. Ueber das Aërenchym, ein dem Kork homologes Gewebe bei Sumpfpflanzen. Jahrb. Wiss. Bot. 20: 526–574.

Schrenk, J. 1889. On the floating tissue of *Nesaea verticillata* (L.) H.B.K. Bull Torrey Bot. Club 16: 315–323.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. Edward Arnold Ltd., London. 610 pp.

Shimamura, S., T. Mochizuki, Y. Nada & M. Fukuyama. 2002. Secondary aerenchyma formation and its relation to nitrogen fixation in root nodules of soybean plants (*Glycine max*) grown under flooded conditions. Plant Prod. Aci. 5 (4): 294–300.

Shimamura, S., T. Mochizuki, Y. Nada & M. Fukuyama. 2003. Formation and function of secondary aerenchyma in hypocotyl, roots and nodules of soybean (*Glycine max*) under flooded conditions. Plant Soil 251: 351–359.

Stevens, K.J., R.L. Peterson & R.J. Reader. 2002. The aerenchymatous phellem of *Lythrum salicaria* (L.): a pathway for gas transport and its role in flood tolerance. Ann. Bot. 89: 621– 625.

Stevens, K.J., R.L. Peterson & G.R. Stephenson. 1997. Morphological and anatomical responses of *Lythrum salicaria* L. (purple loosestrife) to an imposed water gradient. Int. J. Plant Sci. 158: 172–183.

Wilson, M.V.H. 1977. Middle Eocene freshwater fishes from British Columbia. R. Ont. Mus. Life Sci. Contrib. 113: 1–61.

Wilson, M.V.H. 1982. A new species of *Amia* from the Middle Eocene of British Columbia. Palaeontology 25: 413–424.

**Fig. 3.1**. Roots of *Decodon allenbyensis* prior to, and shortly after secondary tissue production. – a: Transverse section of young branching root with early vascular cambium activity; arrow at epidermis with enlarged hypodermal cells beneath; double arrow at early branching young root with unexpanded cortex. P6427 L bot #6. – b: Transverse section of young root with pentarch primary xylem surrounded by dark endodermis, aerenchymatous cortex, and prominent hypodermis (at arrow). P6427 L bot #6. – c: Transverse section of young root with hexarch primary xylem and aerenchyma surrounding the central cylinder. P6019 B #4. – d: Oblique transverse section of young root with septarch primary xylem. P1303 C2 side #2. – e: Young root with aerenchymatous primary cortex with some secondary xylem and early lacunate phellem; inset left: close-up of specimen at epidermal layer; inset right: close-up of the specimen showing edge of secondary xylem, secondary phloem (arrow at phloem fiber bundle), and early lacunate phellem. P6019 B #6. — Scale bar = 200 μm.

Fig. 3.1

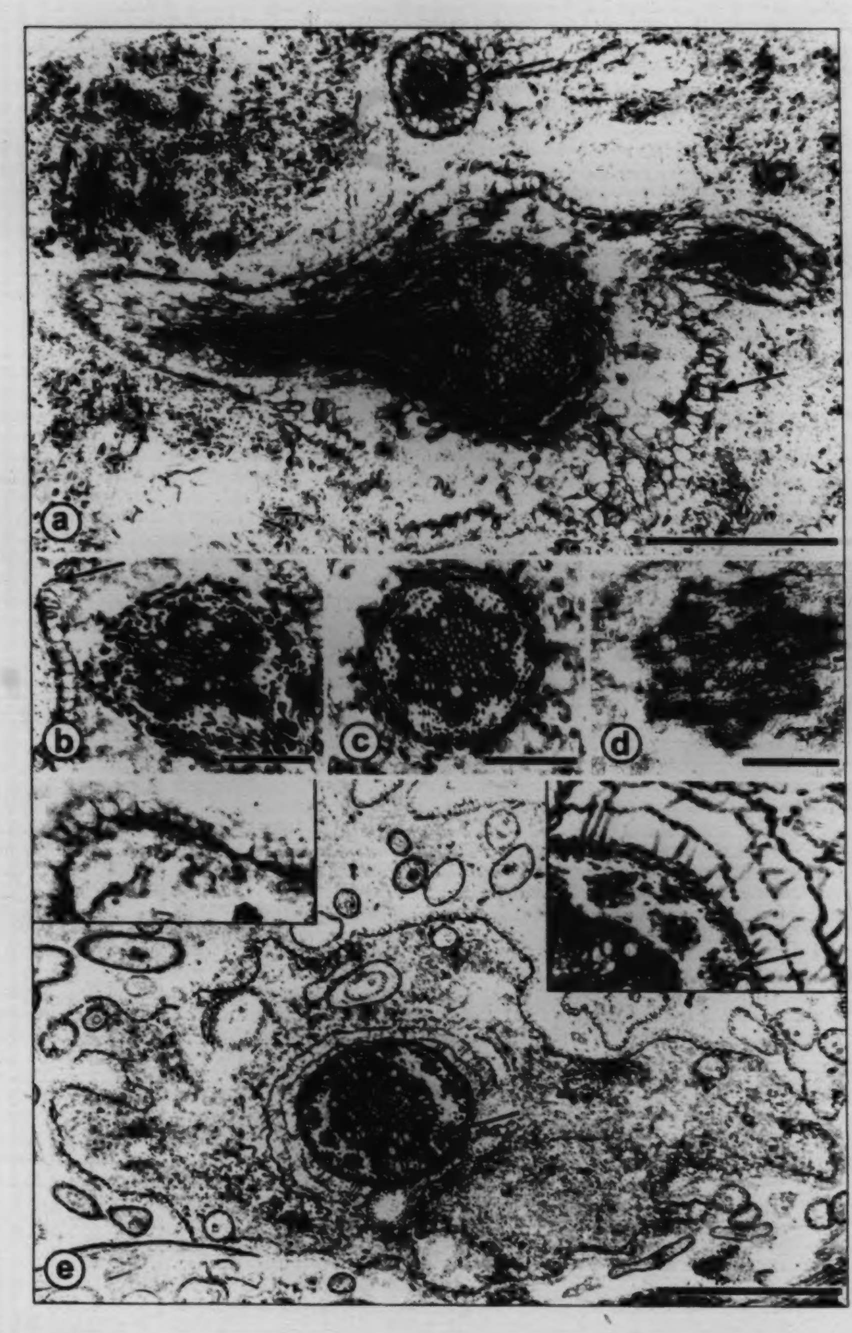


**Fig. 3.2**. Roots of *Decodon allenbyensis*. – a: Young root with limited secondary xylem and extensive thin-walled phellem and several secondary roots. P5956 E bot #3b. – b: Transverse section of xylem, phloem and periderm. Note phloem fiber bundles. P6427 K bot #34. – P = phellem; PH = phloem; X = secondary xylem. — Scale bar = 500 μm.

**Fig. 3.2**

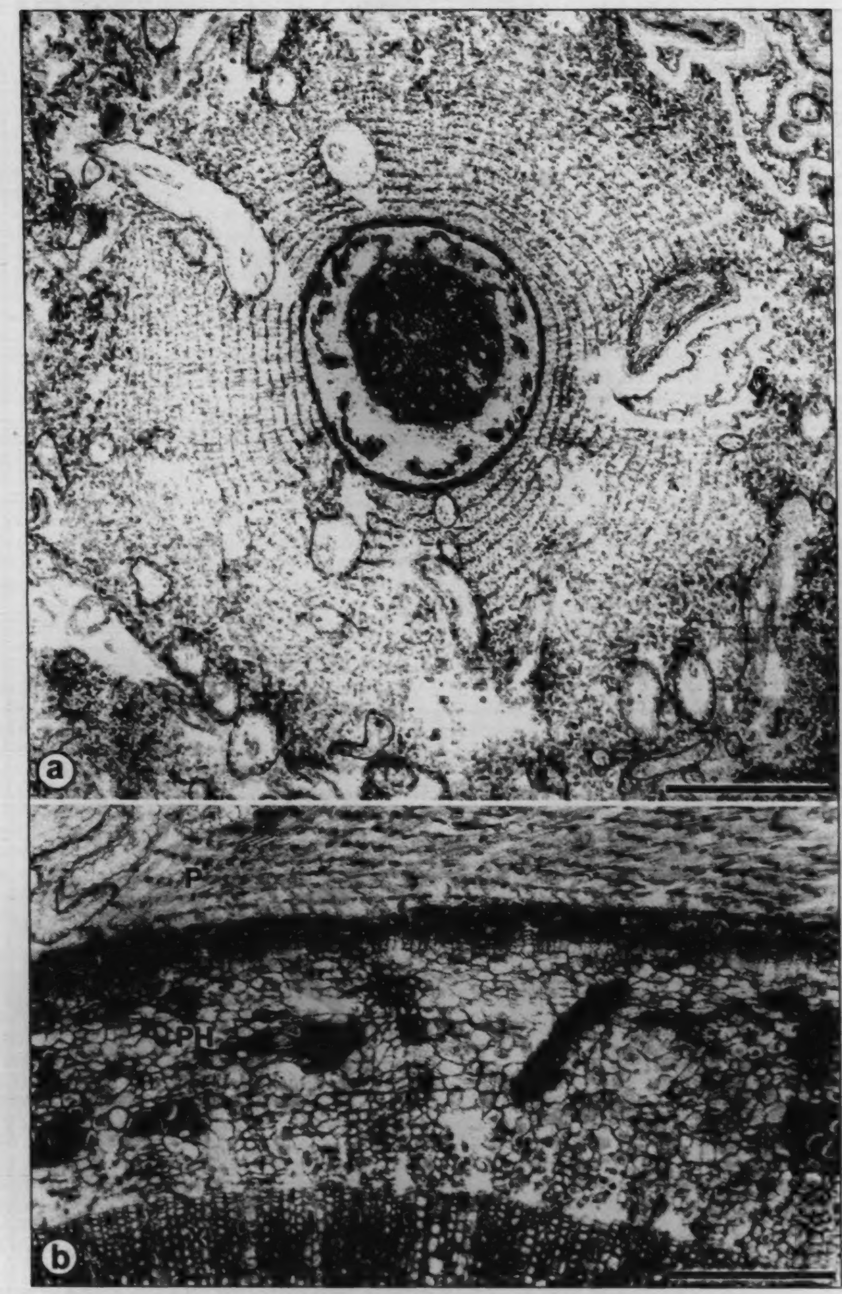


**Fig. 3.3**. Roots of *Decodon allenbyensis*. – a: Transverse section of root with two growth increments, diffuse-porous wood, phloem fiber bundles and abundant thin-walled phellem with layers of dark colored phelloids (arrows). P6019 B #7. – b: Transverse section of root with three growth increments, and extensive thin-walled phellem with several layers of dark colored phelloids (arrows). P5912 H top #3. — Scale bar = 2.5 mm.

Fig. 3.3

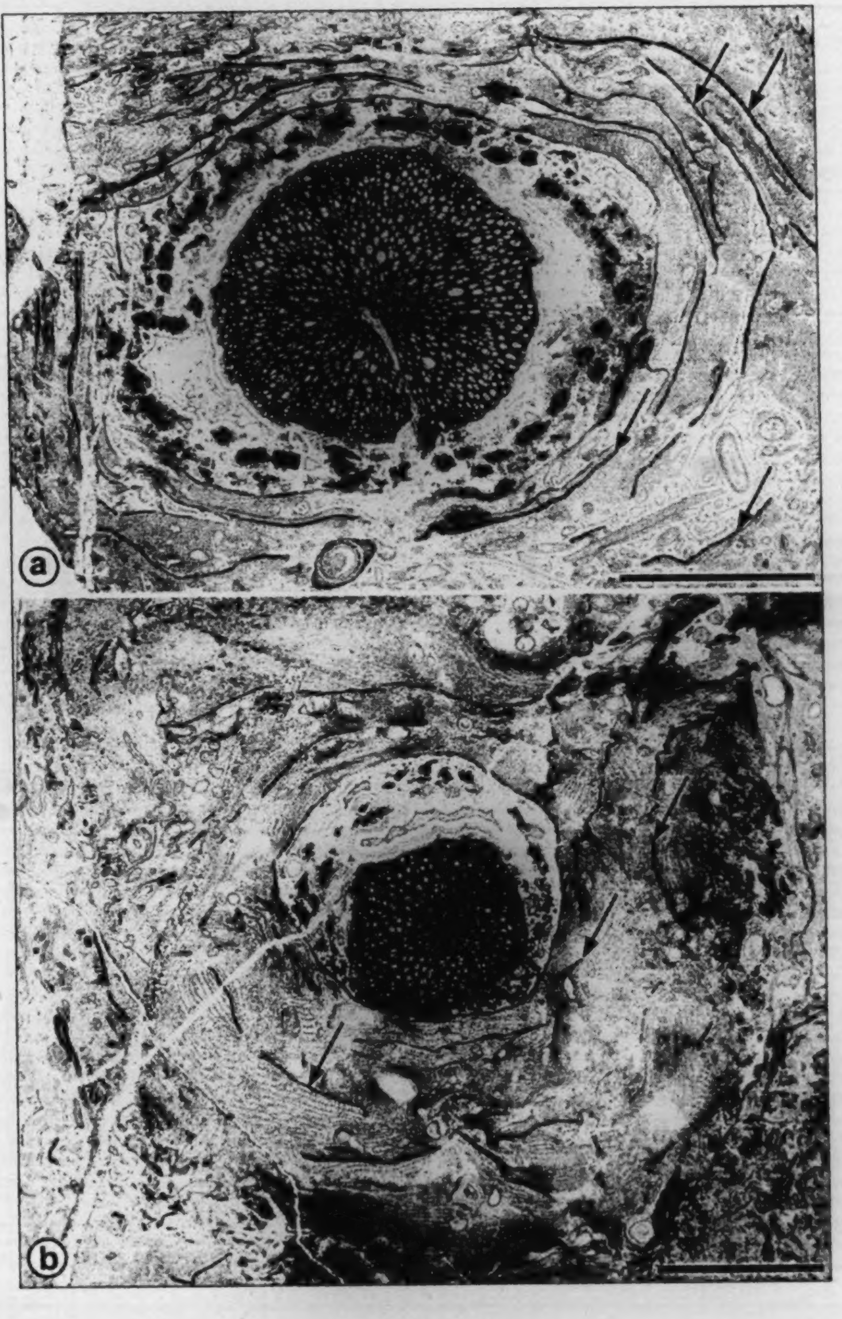


**Fig. 3.4**. Phellem in roots of *Decodon allenbyensis*. – a: Rows of lacunate thin-walled phellem. P6288 A #1. – b: Alternating isodiametric and radially elongate cells of phellem separated by rectangular lacunae. P6288 A #1. – c: Phellem with elongated cells in contact with dark non-aerenchymatous cells representing former location of phellogen. P6288 A #1. — Scale bar = 100 μm.

Fig. 3.4

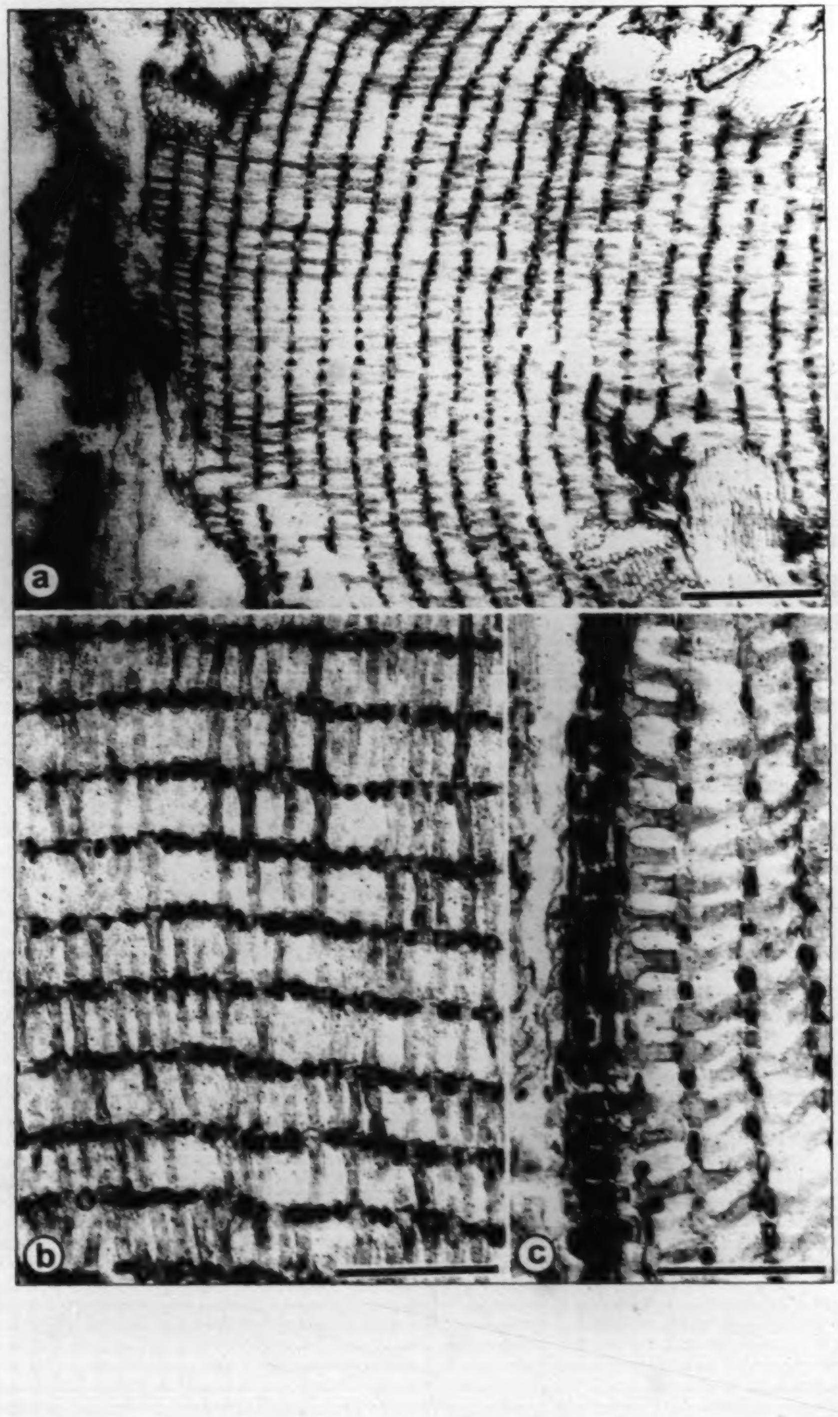


**Fig. 3.5**. Phloem and rhytidome of *Decodon allenbyensis* – a: Radial longitudinal section of secondary xylem and phloem. P6427 K bot #24. – b: Tranverse section of large, crushed stem (at right) with rhytidome to left, composed of zones of old secondary phloem alternating with zones of phelloids (arrows). P6427 L bot #7. – c: Transverse section of lacunate secondary phloem with tangentially elongated cells and clusters of phloem fibers. P6427 L bot #6. – d: Higher magnification of Fig. 3.5c showing tangentially elongated cells alternating with radial rows of small rectangular cells interrupted by phloem fiber bundles. P6427 L bot #6. – P = phellem; PH = phloem; X = secondary xylem. — Scale bar = 500 µm.

Fig. 3.5

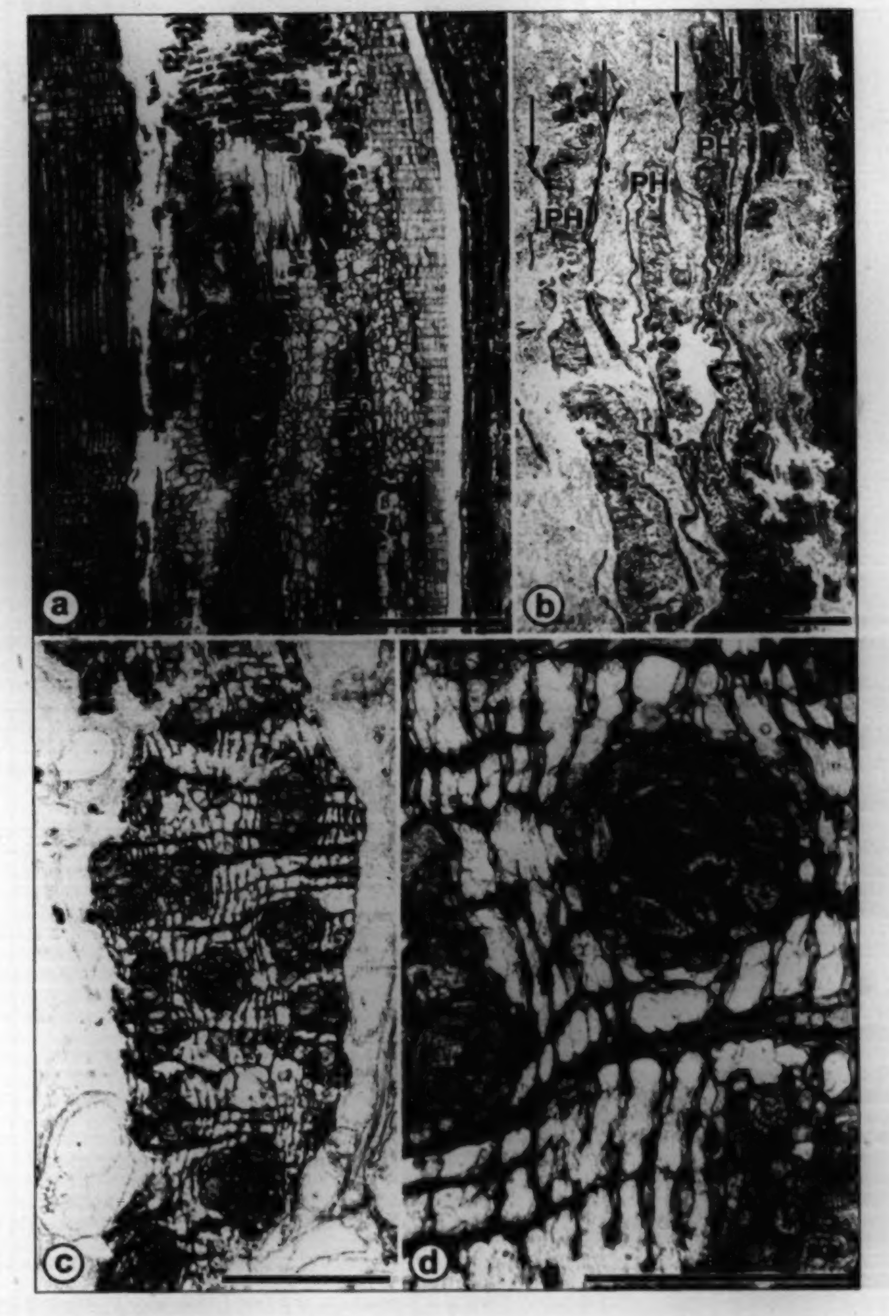


**Fig. 3.6**. Diagram representing *Ludwigia*-type and *Decodon*-type morphogenetic stages in aquatic roots. – A column: *Ludwigia*-type morphogenesis: cells of primary cortex radially elongate, shedding dermal layers to make tiered aerenchyma. True lacunate phellem is produced by phellogen in association with secondary vascular tissues; phellogen is formed in pericycle. – B column: *Decodon*-type morphogenesis: cells of primary cortex form lacunae to make aerenchyma that is contained by dermal layers. Secondary vascular tissues are produced prior to phellogen initiation. Lacunate phellem is then produced by phellogen that is formed in pericycle. — ep = epidermis with hypodermis, pl = phloem, xy = primary xylem, cor = primary cortex, spl = secondary phloem, wo = wood, phe = phellem.

Fig. 3.6

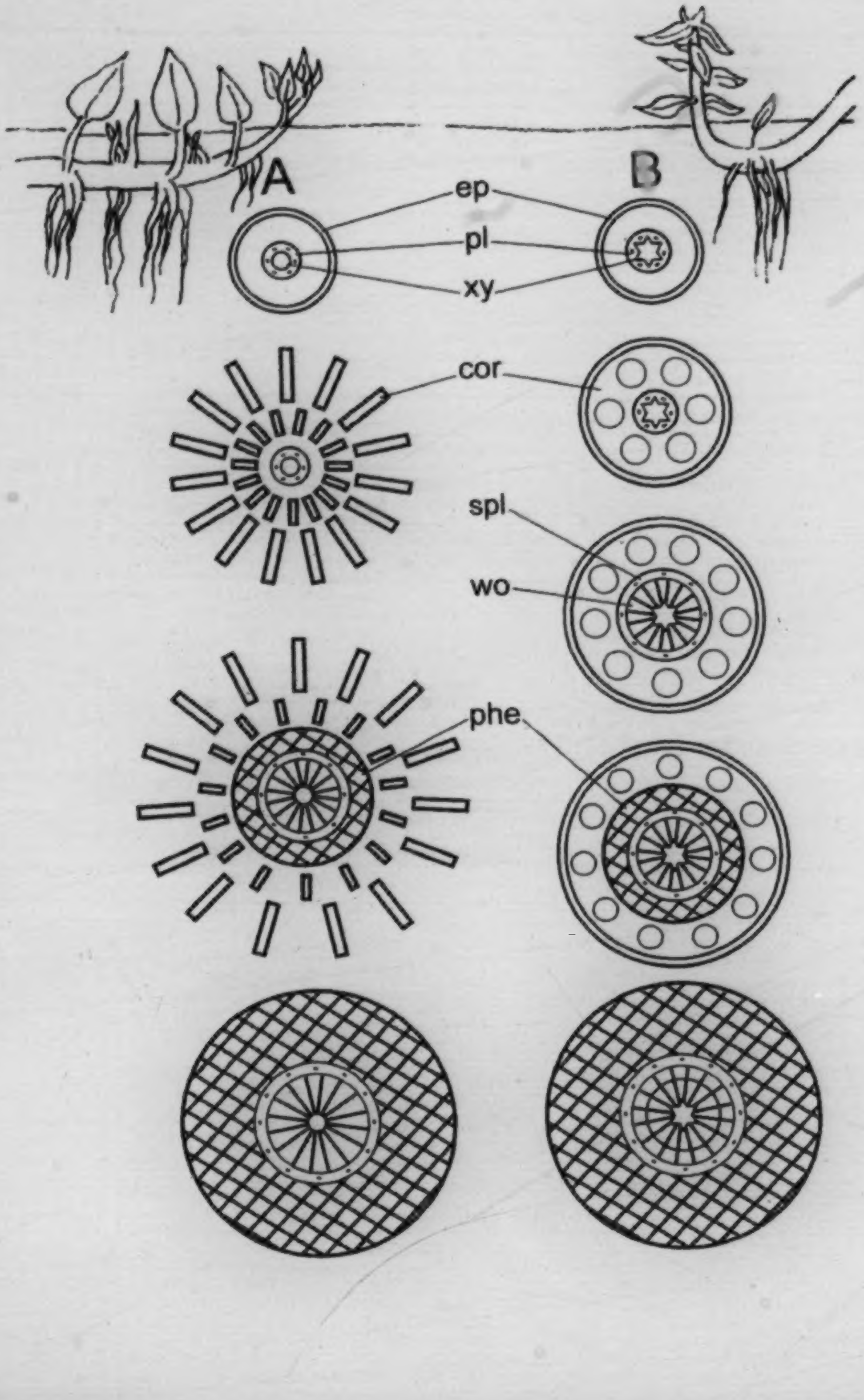
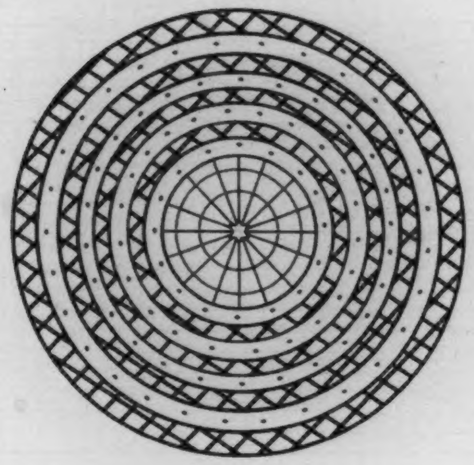


**Fig. 3.7**. Diagram representing complex aquatic rhytidome. This aquatic rhytidome is known only in fossil *Decodon allenbyensis*. Tissues are as in Fig. 3.6, but crosshatch zones represent non-aquatic phelloids, and secondary phloem zones represent aquatic lacunate phloem.

Fig. 3.7



# CHAPTER 4

## *Duabanga*-like leaves and comparative leaf histology of Lythraceae *sensu lato*[1]

### INTRODUCTION

Lythraceae is a large family in the order Myrtales, containing about 600 species that are mainly distributed in tropical to subtropical regions (Graham, 1964; Graham et al., 1993). Punicaceae (*Punica* L.) and Sonneratiaceae (*Sonneratia* L.f. and *Duabanga* Buchanan-Hamilton) have been included in Lythraceae by several authors, sometimes with Trapaceae (*Trapa* L.) (Dahlgren and Thorne, 1984; Thorne, 1992a,b; Graham et al., 1993; Graham, 1999; Judd et al., 1999). Phylogenetic analyses using morphological (Johnson and Briggs, 1984; Graham et al., 1993) and molecular characters, (Conti et al., 1996, 1997; Shi et al., 2000; Huang and Shi, 2002) have resulted in the recognition of a lythraceous clade that also includes *Sonneratia*, *Duabanga*, and *Punica*. Lythraceae sensu lato includes five subfamilies: Lythroideae with 28 genera, and Punicoideae, Sonneratioideae, Duabangoideae, and Trapoideae (Graham et al., 1998), each with a single genus.

The oldest fossil records of Lythraceae are of seeds from the Campanian (Cretaceous) of Mexico (Rodríguez-de la Rosa et al., 1998) and from the Paleocene of southern England (Reid and Chandler, 1933; Chandler, 1961). Fossils of Lythraceae include fruits, seeds, leaves, and pollen (Graham and Graham, 1971; Tiffney, 1981; Muller, 1981; Friis, 1985). Leaves assignable to the genus *Decodon* J. F. Gmelin have been reported from compression/impression fossils from North America (Wolfe and Tanai, 1980; Wehr and Hopkins, 1994; Stockey and Wehr, 1996) and western Europe (Kvaček and Sakala, 1999). However, detailed anatomical data are not known for these leaves and one cannot be certain that they represent this genus. Manchester et al. (1998) point out that assigning isolated leaves of the order Myrtales to extant taxa in the absence of fruit and flower data is not advised because of the similarities in venation pattern in the order. The mosaic of characters seen in fossil myrtalean taxa such as *Syzygioides* Manchester, Dilcher et Wing (1998) illustrate that with isolated organs, fossils of Myrtales may be difficult to assess and that whole plant reconstructions are necessary.

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[1] A version of this chapter has been published. Little, Stockey and Keating 2004. American Journal of Botany. 91: 1126-1139.

In this paper, a lythraceous leaf type from the Middle Eocene Princeton chert of British Columbia, Canada is described. These leaves are closely associated in the same chert layers with fruits, seeds, and recently described vegetative axes with lacunate phellem, of *Decodon allenbyensis* Cevallos-Ferriz et Stockey (Cevallos-Ferriz et Stockey, 1988; Little and Stockey, 2003). This study compares the fossil leaves to those of Myrtales histologically, and in particular to those of Lythraceae sensu lato, using characters described by Keating (1984), and using new characters, to assess their affinities. This comparison, along with original observations of *Decodon verticillatus* (L.) Ell. leaves, demonstrates newly recognized diversity in Lythraceae of the Middle Eocene of western North America.

## MATERIALS AND METHODS

Permineralized leaf specimens studied here come from the Princeton chert locality on the east bank of the Similkameen River, 8.4 km southwest of Princeton, British Columbia (UTM 10U FK 786725; 49° 22' 33" N 120° 32' 18" W). The chert is part of the Allenby Formation of the Princeton Group and is dated at 48.7 million years bp (Hills and Baadsgaard, 1967; H. Baadsgaard, University of Alberta, pers comm, 1999). Leaves come from layer #43 of the chert and are most often associated with the fruits, seeds and vegetative axes of *Decodon allenbyensis* (Little and Stockey, 2003) as well as the fruits and seeds of *Paleomyrtinaea princetonensis* Pigg, Stockey et Maxwell (1993).

Fossil specimens were prepared with the cellulose acetate peel technique (Joy et al., 1956) modified for hydrofluoric acid (Basinger and Rothwell, 1977; Basinger, 1981). Peel sections were mounted with Eukitt rapid mounting medium (O. Kindler GmbH & Co., Freiburg, Germany) for microscopic examination. All fossil specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Slides of extant Myrtales were examined from the material sectioned by Keating (1984). The sample of species of Lythraceae sensu lato were originally illustrated by camera lucida, but are photographed for the first time here, and additional data are provided based on these microscopic sections. Leaves were preserved in FAA or FPA, embedded in paraffin, sectioned at 10 µm and stained with safranin-O/fast green FCF (Keating, 1984). All leaves were sectioned at midlevel in transverse section (Keating, 1984). The sections of extant leaves used in this study are currently housed at the University of Alberta.

Leaves of extant *Decodon verticillatus,* examined here for the first time, were studied using paraffin-embedded sections stained with safranin-O/fast green FCF (Johansen, 1940). In addition, leaves of extant *D. verticillatus* were examined by Cryo-SEM using an EMJTECK (K1250) cryosystem, and the chromium trioxide technique (Alvin and Boulter, 1974). Samples were coated with 15 nm Au with a Nanotek sputter coater, and viewed with a Japan Electronics Optics Ltd. (JEOL) Scanning Electron Microscope (JSM 6301) at 5 kV. Images were taken with a Leaf Microlumina System version 1.2 (Leaf Systems Inc.,Westborough, Massachusetts ) and a Phase One digital studio camera (Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe Photoshop (Adobe Systems Inc., San Jose, California)

## RESULTS

***Fossil leaves*** – Leaves are often found as isolated fragments and in small groups that are associated with roots and stems of *Decodon allenbyensis*; however they have not been found in attachment (Fig. 4.1). The longest leaf found (ca. 26 mm long) is also the most intact in transverse section (Fig. 4.2). Leaves were degraded prior to preservation, and midribs are not complete for all tissues in a given specimen (Figs. 4.3, 4.4). Fine venation observed in paradermal section shows polygonal areolation with freely ending veinlets (Fig. 4.6).

The lamina is dorsiventral and 180 – 270 μm thick (Figs. 4.7, 4.8). The epidermis is often missing in the fossil leaves (Fig. 4.5). Adaxial epidermal cells are rectangular to rounded; enlarged epidermal cells with contents have not been observed (Figs. 4.7, 4.8). The abaxial epidermis is papillate (Figs. 4.7, 4.8), but is non-papillate over the midribs and ribs of major veins (Fig. 4.3). Cells of the adaxial epidermis are larger than those of the abaxial epidermis. Prominent overarching papillae are observed in the abaxial epidermis, and these areas probably represent the positions of stomata (Figs. 4.7, 4.8, arrows). Multicellular trichomes and cuticle were not observed.

The mesophyll is well differentiated into a double-layered palisade, that makes up 50% of the lamina thickness; spongy layers are five to seven cells thick at the lamina. Midribs are flat to convex adaxially and prominently rounded/convex to V-shaped abaxially (Figs. 2, 3, 4). Midvein xylem and phloem are rarely well preserved, possibly degraded by fungi (Figs. 4.3, 4.4). Although preservation makes observation of midvein and surrounding tissues difficult, midveins appear to be C-shaped, incurved adaxially, surrounded by periphloic fibers except for an adaxial gap, and surrounded by ground tissue (Fig. 4.3, 4.4). Secondary vein ribs are flat adaxially and abaxially convex or slightly biconvex with C-shaped secondary veins that are surrounded by fibers (Table 4.1). Minor veins are also surrounded by fibers (Fig. 4.5). Crystals were not observed in the leaves.

Many of the fossil leaves have tissues invaded by septate fungal hyphae. Dark-colored hyphal masses, almost exclusively on the abaxial side of the lamina, invade and replace the papillate epidermal cells and mesophyll tissue (Figs. 4.9, 4.10). Sexual spores and/or conidia from these dark sterile stromata were not observed.

***Leaves of* Decodon verticillatus *(L.) Ell.*** – In surface view, anomocytic stomata are level with the epidermis and occur on both leaf surfaces (Figs. 4.11–4.14). Epidermal cells appear polygonal when observed with cryo-SEM, with a clear outline and smooth surface (Figs. 4.13, 4.14). Isolated, dried cuticle observed with SEM appears striated/wrinkled, and the outline of the epidermal cells is often less clear (Figs. 4.11, 4.12). Multicellular, branched trichomes occur on both leaf surfaces (Fig. 4.14) and are more dense on or near veins. Fine ornamentation is visible on the trichomes (Figs. 4.14).

In transverse section, leaves are up to 20 mm wide (Fig. 4.15). The lamina is dorsiventral and 110–125 μm thick. The adaxial and abaxial epidermis is similar in thickness and made up of rectangular to rounded cells, with some enlarged, mucilage-filled cells (Fig. 4.16). Some epidermal cells contain spherical clusters of birefringent crytstals (Table 4.1). Trichome ornamentation in sections is not as clear as when viewed with SEM (Fig. 4.15). The mesophyll is well differentiated into a single palisade that makes up 50% of the lamina thickness, and spongy layers three cells thick. Midribs are prominently ridged adaxially and convex/trapezoidal abaxially (Fig. 4.15). Midveins are C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are ridged adaxially and convex/trapezoidal abaxially, similar to midribs (Table 4.1), with weakly C-shaped secondary veins. Druses are observed in the midrib ground tissue and the mesophyll.

***Leaves of other extant Lythraceae*** – *Duabanga grandiflora* (Roxb. ex DC) Walpers – The two specimens examined had some differences. The lamina is dorsiventral and 180–225 μm (Fig. 4.17, 4.18) or 285–335 μm thick (Figs. 4.30, 4.31). Epidermal cells are rectangular to rounded with some cells enlarged and mucilaginous. Cells of the adaxial epidermis are about twice as large as abaxial epidermal cells. Abaxial epidermal cells are papillate (Figs. 4.18, 4.20) over the lamina, but non-papillate on midribs and secondary vein ribs. The cuticle is thin to thick and smooth, or ornamented on the abaxial papillae. Stomata are only found on the abaxial surface, with guard cells level with epidermis, and the surrounding papillate cells overarching the guard cells (Figs. 4.18, 4.20). Trichomes are not present. The well-differentiated mesophyll is a palisade layer, two or two-three cells thick, that makes up 40–50% of the lamina thickness, and spongy layers four to nine cells thick (Fig. 4.18). Midribs are slightly grooved to flat adaxially and V-shaped abaxially (Fig. 4.17) or convex/round to flat adaxially and V-shaped abaxially (Figs. 4.19). Midveins are C-shaped, incurved adaxially, bicollateral, and surrounded by periphloic fibers except for an adaxial gap. Midveins are surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially convex or slightly biconvex (Table 4.1), with C-shaped secondary veins that are surrounded by fibers (Figs. 4.17, 4.19). Druses are observed in midrib and mesophyll tissues.

*Duabanga moluccana* Bl. – The two specimens examined had some differences. The lamina is dorsiventral and 140–190 µm or 260–310 µm thick (Figs. 4.21, 4.22). Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Cells of the adaxial epidermis are about twice as large as those of the abaxial epidermis. The cuticle is thick and ornamented. One specimen has stomata only on the abaxial surface, the other specimen is amphistomatic. Guard cells are level with the epidermis or slightly sunken into the epidermal cells in adaxial stomata. Trichomes were not observed. The mesophyll is well differentiated into a palisade, two or two to three cells thick, that makes up 40–50% of the lamina thickness, and spongy layers four to six cells thick (Fig. 4.22).

Midribs are flat adaxially and convex/rounded abaxially in one specimen (Fig. 4.21). The other specimen has a midrib that is convex adaxially and convex/square abaxially. The bicollateral midveins form a cylinder surrounded by periphloic fibers and ground tissue. Secondary vein ribs are flat adaxially and abaxially convex, with C-shaped secondary veins that are surrounded by periphloic fibers, abaxial ground tissue, and a parenchymatous adaxial extension (Table 4.1). Druses are observed in midrib and mesophyll tissues.

*Lythrum alatum* var. *lanceolatum* (Ell.) Rothrock – The lamina is dorsiventral and 120-130 μm thick (Fig. 4.23). Adaxial and abaxial epidermis is similar in thickness with rectangular to rounded cells, and with some enlarged and mucilaginous cells. Some epidermal cells contain spherical clusters of birefringent crystals. The cuticle is thin and appears striated. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes were not observed. The mesophyll has one distinct palisade layer, occasionally with a less well-differentiated layer below, together the layer(s) make up 30% of the lamina thickness. Spongy mesophyll is three cells thick. Midribs are sunken, grooved adaxially, and slightly V-shaped abaxially (Fig. 4.23). Midveins are short arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are slightly biconvex with small and circular secondary veins (Table 4.1). Druses are observed in the midrib ground tissue and the mesophyll.

*Nesaea longipes* A. Gray – The lamina is dorsiventral and 180–260 μm thick (Fig. 4.24). Adaxial and abaxial epidermis is similar in thickness, with rectangular to rounded cells, and with some enlarged mucilaginous cells. The cuticle is thin and appears striated.

Leaves are amphistomatic with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated with a single palisade layer, that makes up 30% of the lamina thickness. Spongy mesophyll is five cells thick. Midribs are flat, level adaxially, and slightly convex abaxially (Fig. 4.24). Midveins are weak arcs, bicollateral and surrounded by ground tissue. Secondary vein ribs are slightly biconvex with circular secondary veins (Table 4.1). Druses are observed in the midrib ground tissue and mesophyll.

*Ammannia coccinea* Rottb. – The lamina is dorsiventral and 130–160 µm thick (Fig. 4.25). Adaxial epidermal cells are larger than cells of the abaxial epidermis. Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Some epidermal cells contain spherical clusters of birefringent crytstals. Cuticle is very thin and smooth. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated with a single palisade layer, that makes up 50% of the lamina thickness. Spongy mesophyll is three to five cells thick at the lamina. Midribs are concave/grooved adaxially, and rounded/convex abaxially (Fig. 4.25). Midveins are weak arcs, bicollateral and surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially, with circular secondary veins (Table 4.1). Druses are observed in the midrib ground tissue and mesophyll.

*Cuphea spectabilis* S. Graham – The lamina is dorsiventral and 120–160 µm thick (Fig. 4.26). Adaxial epidermal cells are slightly larger than cells of the abaxial epidermis. Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Cuticle is very thin and smooth. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes are uniseriate, one to four celled, and thin walled. The mesophyll is well differentiated with a single palisade layer, that makes up 30% of the lamina thickness. Spongy mesophyll is five cells thick. Midribs are concave/grooved adaxially, and convex/square abaxially (Fig. 4.26). Midveins are weak arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are adaxially grooved and abaxially convex, similar to midribs, with weakly C-shaped secondary veins surrounded by ground tissue (Table 4.1). Druses are observed in the midrib ground tissue and mesophyll.

*Heimia salicifolia* (H.B.K.) Link. – The lamina is dorsiventral, 100–125 µm thick (Fig. 4.27). Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Adaxial epidermal cells are slightly larger than those of the abaxial epidermis. The cuticle is thin, striated, and ornamented. Stomata are found only on the abaxial surface with guard cells level with the epidermis. Trichomes are not present. The well-differentiated mesophyll is a single palisade layer, that makes up 30% of the lamina thickness, and a spongy layers three to five cells thick. Midribs are concave/grooved adaxially, and V-shaped abaxially (Fig. 4.27). Midveins are weakly C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are adaxially and abaxially convex with weakly C-shaped secondary veins surrounded by ground tissue (Table 4.1). Druses are observed in the midrib ground tissue and mesophyll.

*Lagerstroemia speciosa* (L.) Pers. – The lamina is dorsiventral and 180–210 µm thick (Fig. 4.28). Epidermal cells are rectangular to rounded, with periclinally divided cells occurring regularly. Some epidermal cells contain spherical clusters of birefringent crystals and some cells are enlarged and mucilaginous. The mucilage cells tend to protrude into the mesophyll and sometimes appear to be below the epidermis. Cells of the adaxial epidermis are about twice as large as those of the abaxial epidermis. The cuticle is thin, smooth and slightly ornamented. Stomata are found only on the abaxial surface with guard cells level with the epidermis. Trichomes are uniseriate, one to four celled, and thin walled. The mesophyll is well differentiated, composed of a double palisade layer that makes up 40% of the lamina thickness, and spongy layers four to six cells thick. Midribs are convex/rounded adaxially, and convex/square abaxially (Fig. 4.28). Bicollateral midveins form a cylinder surrounded by periphloic fibers and ground tissue. Secondary vein ribs are flat adaxially and abaxially convex, with weakly C-shaped secondary veins that have an abaxial band of periphloic fibers, abaxial ground tissue, and a parenchymatous adaxial extension (Table 4.1). Prismatic crystals and druses are abundant in midrib and mesophyll tissues.

*Lafoensia speciosa* (H.B.K.) DC – The lamina is dorsiventral and 130–185 µm thick (Fig. 4.29). Adaxial and abaxial epidermis are similar in thickness, with rectangular to rounded cells, and with some enlarged mucilaginous cells. Some epidermal cells contain spherical clusters of birefringent crytstals. Cuticle is thin and smooth. Stomata are found only on the abaxial surface with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated, with a single palisade layer that makes up 25% of the lamina thickness, and spongy layers six to eight cells thick. Midribs are grooved adaxially and convex/rounded abaxially (Fig. 4.29). Midveins are C-shaped, bicollateral with an abaxial band of periphloic fibers, and surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially convex, with weakly C-shaped secondary veins that have an abaxial band of periphloic fibers, abaxial ground tissue, and a parenchymatous adaxial extension (Table 4.1). Prismatic crystals and druses are abundant in midrib and mesophyll tissues.

*Lawsonia inermis* L. – The lamina is dorsiventral and 180–210 μm thick (Fig. 4.30). Adaxial and abaxial epidermis are similar in thickness, with rectangular to rounded cells, with some enlarged mucilaginous cells. The cuticle is thin, smooth or slightly ornamented. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes are not present. The mesophyll cells are dense, with a single palisade layer, occasionally double, that makes up 30–40% of the lamina thickness; spongy layers are four to six cells thick. Midribs are convex/rounded adaxially and convex/rounded abaxially (Fig. 4.30). Bicollateral midveins are C-shaped and surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially, with circular secondary veins (Table 4.1). Druses are observed in midrib and mesophyll tissues.

*Punica protopunica* Balf. f. – The lamina is dorsiventral, tending to isobilateral, and 230-290 μm thick (Fig. 4.31). Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Adaxial epidermal cells are about twice as large as abaxial epidermal cells. The cuticle is thick and ornamented. Stomata are only found on the abaxial surface with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated into a palisade that is two or three cells thick, that makes up 30–40% of the lamina thickness and spongy mesophyll five to eight cells thick. The three most abaxial spongy mesophyll layers are densely packed and rectangular, imparting a partially isobilateral appearance to the lamina. Midribs are slightly convex to flat adaxially and convex/round abaxially (Fig. 4.31). Midveins are weak arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are slightly convex adaxially and abaxially, similar to midribs, with weakly C-shaped secondary veins that have a parenchymatous adaxial extension (Table 4.1). Prismatics are observed in mesophyll tissues.

*Punica granatum* L. – The lamina is dorsiventral and 345–380 μm thick (Fig. 4.32). Epidermal cells are rectangular to rounded, and no enlarged mucilaginous cells were observed. Cells of the adaxial epidermis are larger than those of the abaxial epidermis. Cuticle is thin, smooth to slightly ornamented. Stomata are found only on the abaxial surface, with guard cells level with the epidermis. Trichomes were not observed. The well-differentiated mesophyll is a single palisade layer, about 40–50% of the lamina thickness, and spongy layers three to four cells thick. Midribs are slightly concave to flat adaxially and convex/round abaxially (Fig. 4.32). Midveins are C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are flat adaxially and slightly convex/rounded abaxially with weakly C-shaped to circular secondary veins (Table 4.1). Prismatics and druses are observed in midrib and mesophyll tissues.

*Sonneratia* sp. – The lamina is dorsiventral, tends toward isobilateral, and is 325–415 μm thick (Fig. 4.33). Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells that intrude into the mesophyll appearing to be just internal to the epidermis. Adaxial and abaxial epidermal cells are similar in size. The cuticle is thick and ornamented. Leaves are amphistomatic, and guard cells are slightly sunken with slightly overarching subsidiary cells. Trichomes were not observed. Mesophyll is well differentiated into a palisade three to four cells thick, that makes up 25–30% of the lamina thickness, and spongy layers 10–12 cells thick. The lowest three to four mesophyll layers are densely packed and rectangular, imparting a partially isobilateral appearance to the lamina. Midribs are slightly flat to concave adaxially and convex/round to V-shaped abaxially (Fig. 4.33). Midveins are C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are not apparent with the C-shaped secondary veins embedded in the mesophyll (Table 4.1). Sclereids are observed in the mesophyll, and druses in the midrib and mesophyll tissues.

*Sonneratia apetala* Buch.-Ham. – The lamina is isobilateral and 244–510 μm thick (Fig. 4.34). Epidermal cells are rectangular to rounded, with enlarged mucilaginous cells intruding into the mesophyll appearing just internal to the epidermis. Abaxial and adaxial epidermal cells are similar in size. Cuticle is thick and ornamented. Leaves are amphistomatic, and guard cells are slighly sunken, with slightly overarched subsidiary cells. Trichomes are not present. Well-developed adaxial and abaxial palisade, both three cells thick, together make up 50–60% of the lamina thickness. Spongy mesophyll layers are five to eight cells thick. Midribs are convex/round adaxially and abaxially (Fig. 4.34). Bicollateral midveins form a cylinder, surrounded by ground tissue. Secondary vein ribs are not apparent with the C-shaped secondary veins embedded in the mesophyll (Table 4.1). Sclereids are observed in the mesophyll and druses in the midrib and mesophyll tissues.

## DISCUSSION

Permineralized plant remains from layer # 43, the most extensively surveyed of the outcrop, include the following taxa: monocots, Araceae and Alismatales (Currah and Stockey, 1991; Smith and Stockey, 2003.); *Allenbya*, Nymphaeaceae (Cevallos-Ferriz and Stockey, 1989.); *Eorhiza arnoldii*, incertae sedis (Robison and Person, 1973; Stockey and Pigg, 1994); *Paleomyrtinaea*, Myrtaceae (Pigg et al., 1993); and *Decodon allenbyensis* (Cevallos-Ferriz and Stockey, 1988; Little and Stockey, 2003). Of these taxa, the leaves are hypothesized to belong to *Decodon* on the basis of their lythraceous features and close association to abundant fruits, seeds, stems, and aquatic stems and roots of this taxon (Little and Stockey, 2003). Other dicots of layer # 43, either have leaves that are already known (i.e., *Eorhiza arnoldii*), or would likely have dissimilar leaves (i.e., Nymphaeaceae and monocots) to the fossil leaves described here. Finally, the most closely related taxon to *Decodon, Paleomyrtinaea* (Myrtales), a guava-like plant, is unlikely to have this leaf type because the fossil leaves lack secretory canals and hypodermis, features that are typically found in the mesophyll of many Myrtaceae (Keating, 1984). For these reasons it is likely that these leaves belong to *Decodon allenbyensis*, if not some other unknown taxon.

The fossil, *Decodon allenbyensis*, has wood and periderm anatomy in its stems and roots that is very similar to that seen in extant *D. verticillatus* (Little and Stockey, 2003). Therefore, leaves of *D. verticillatus*, the only living species in the genus, were assessed for any diagnostic, anatomical characters that may serve to link the fossil leaves with the *D. allenbyensis* axes. However, leaves of *D. verticillatus* have distinctive leaf anatomy in Lythraceae, and differ from the fossil leaves (Table 4.1). The adaxially-ridged midribs and secondary vein ribs of *D. verticillatus* are distinctive in shape and prominence, whereas, the fossils have adaxially convex/round midribs and adaxially flat secondary vein ribs. This adaxial midrib and secondary vein rib shape is unlike those found in other Lythraceae. The trapezoidal abaxial midrib in *D. verticillatus*, is most similar to the square shaped midrib of *Cuphea spectabilis* or *Lafoensia speciosa,* and is unlike midribs of the fossil leaves that are abaxially convex/round to V-shaped (Table 4.1). Secondary vein ribs with a trapezoidal abaxial shape also appear to be diagnostic for *D. verticillatus*. *Decodon verticillatus* has a single palisade layer and no extraxylary fibers around its veins, traits common in Lythraceae (Table 4.1), and the large multicellular hairs are similar to those seen in *Lagerstroemia* (Solereder, 1908; Gin, 1909; Metcalfe and Chalk, 1950). However, the fossil leaves have fibers around veins, a double palisade, and lack muticellular trichomes.

Isolated *Decodon verticillatus* cuticle viewed with SEM has striations, but fresh leaf surfaces with cryo-SEM have no striations. These striations, an artifact of dessication due to the thin and delicate cuticle, may be misinterpreted as cuticle ornamentation in Lythraceae, where true ornamentation also occurs. Kvaček and Sakala (1999) observed striated cuticle from preparations of Miocene *Decodon* from northern Bohemia. These leaves were borne on axes bearing fruits. The striations were used to identify other isolated foliage with similar venation to *Decodon gibbosus* (Reid) Reid in Nitikin (Kvaček and Sakala 1999). One cannot debate that the leaves attached to fruits with seeds, from the Miocene of Northern Bohemia, are those of *Decodon*. However, many leaves in Order Myrtales tend to have similar venation (Manchester et al., 1998), and cuticle thickness may vary depending on environmental conditions. Therefore, striations alone cannot distinguish *Decodon* from other Myrtales in the fossil record. Using striations as a taxonomic character has been avoided in this study and I suggest that using them to identify and link isolated fossil leaves of Myrtales may prove spurious without further evidence such as, anatomy or attachments of leaves to reproductive structures.

The fossil leaves fit well into the general range of characters seen in Myrtales (Keating, 1984) and appear to be most similar to those of Lythraceae. Lythraceae typically have adaxially grooved to convex, and abaxially convex/rounded midribs, with C-shaped midveins, rounded to rectangular epidermal cells, and one to three palisade layers (typically 1 or 2 in a given leaf) (Solereder, 1908; Gin, 1909; Metcalfe and Chalk, 1950; Keating, 1984). Within this family several anatomical features, such as extraxylary fiber distribution, presence of leaf sclereids, and trichomes are diagnostic (Table 4.1). Enlarged mucilage-filled cells, often in the epidermis, are considered diagnostic for Lythraceae within Order Myrtales (Keating, 1984). However, these have not been observed in the fossil leaves and well-preserved epidermis is rare.

The combination of characters seen in the fossils is most similar to *Duabanga grandiflora*, sharing 16 of 22 characters (Table 4.1). Leaves of *D. grandiflora* and the fossils have the same number of palisade layers, type of midrib and midvein shape, midvein fibers, and the same secondary vein and secondary vein rib shape. Fossil leaves and leaves of *D. grandiflora* have overlapping ranges in midrib shape and in the number of spongy mesophyll layers (Table 4.1). Variability of observed fossil midrib shapes may be due, in part, to the placement of the section, as the midrib shape may change from the petiole to the apex, and the exact level of sectioning is unknown for the fossil leaves. *Punica protopunica* shares 10, and *Duabanga moluccana* shares 13 characters with the fossil leaves. If one includes overlapping ranges of features such as number of mesophyll layers and midrib shape, along with shared qualitative features, such as presence or absence of druses, the fossils share six to eight characters with the most of the extant taxa surveyed here (Table 4.1).

Fossil leaves and leaves of *Duabanga grandiflora* share a distinctive papillate abaxial epidermis among all the leaves described. These unique papillae were called "long mamilliform papillae" by Solereder (1908) and "mamilliforme" by Gin (1909). Solereder (1908) stated that this type of epidermis is diagnostic for *Duabanga*. In this study, we observed it only in one species, *D. grandiflora*, but not in *D. moluccana* (Table 1). Abaxial epidermal papillae are also reported in other Myrtales, including species of *Olinia* (Oliniaceae) (Mujica and Cutler, 1974) and in *Crypteronia paniculata* (Crypteroniaceae) (Gin, 1909). However, when present in *Olinia*, they are more irregular and less elongate than in the fossil leaves. *Olinia* leaves further differ from the fossils in having a hypodermis over the veins and at the laminar margins, sclereids in the mesophyll, distinct angular epidermal cells, and thick cuticles (Mujica and Cutler, 1974). *Crypteronia paniculata* abaxial papillae resemble small, uniseriate trichomes with attenuate tips and occur occasionally (Gin, 1909), in contrast to the distinctive "mamilliform" papillate abaxial epidermal cells present throughout the lamina of the fossil leaves. This taxon also differs from the fossil in having a circular midvein and regular rectangular epidermal cells (our observation from Myrtales leaf slide collection).

Diffuse mesophyll sclereids are mentioned as characters for Sonneratiaceae (Rao and Das, 1979) (comprised by *Duabanga* and *Sonneratia*). In contrast, diffuse sclereids were observed only in *Sonneratia* in this study (Table 4.1).

Types of crystals are taxonomically important for families of Myrtales (Mujica and Cutler, 1974; Keating, 1984). For example, raphides in Myrtales are found only in Onagraceae (Keating, 1982). Druses occur in all lythraceous taxa, but prismatic crystals were restricted to a few taxa (Table 4.1). Epidermal cells containing birefringent crystals were also observed for certain lythraceous taxa (Table 4.1). Unfortunately, the silicification that formed the chert, as well as the HF etching in the cellulose acetate peel technique makes observation of crystals in Princeton chert fossils unlikely.

Trichomes are diverse in Lythraceae and are used to identify and describe taxa (Koehne, 1903). Amarasinghe et al. (1991) systematically surveyed trichome types in the genus *Cuphea* and found them to be valuable taxonomic characters. Although the data does not at first indicate the importance of trichomes (Table 4.1), certain types of trichomes such as globose multicellular trichomes in *Woodfordia* Salisb., *Lourtella* S.A.Graham, P.Baas & H.Tobe, *Adenaria* H. B. K., *Koehneria* S.A.Graham, H.Tobe & P.Baas, *Pehria* Sprague, and possibly *Cuphea* P.Browne are likely a synapomorphy for the clade containing these taxa (Graham et al., 1993; S. A. Graham, Missouri Botanical Garden, pers comm, 2003). Therefore, further systematic studies of leaf and floral indument may yield more taxonomically useful characters, as well as characters for phylogenetic analyses.

The large number of anatomical similarities between the fossil leaves and those of *Duabanga grandiflora*, especially the diagnostic papillate abaxial epidermis, may indicate that a *Duabanga*-like plant was present at the Princeton chert locality during the Middle Eocene. Because extant species of *Duabanga* range from the rainforest region of southeastern Himalaya to New Guinea (Jayaweera, 1967), the presence of these fossil leaves supports the interpretation that Princeton was more tropical in the Middle Eocene (Pigg and Stockey, 1996). If these fossil leaves are *Duabanga*, then this is the only macrofossil record for the genus. However, it is more probable that these leaves are those of *Decodon allenbyensis*. This idea is supported by the mutual abundance and close association of these leaves and in situ roots, isolated stems, and fruits of *Decodon* in layer #43 (Little and Stockey, 2003). Because the chert represents a near-shore lacustrine environment (Cevallos-Ferriz et al., 1991), one would expect the leaves to have been deposited parautochthonously and preserved along with the other above-ground organs (Little and Stockey, 2003). If this hypothesis is supported by future work, then *Decodon allenbyensis* possesses a combination of characters not known for any living Lythraceae: it is similar in growth habit and wood, fruit and seed anatomy to *Decodon*, but has *Duabanga*-like leaves.

The reconstruction of *Decodon allenbyensis* will become increasingly valuable for cladistic analyses. As demonstrated by Huelsenbeck (1991), a fossil taxon, complete in its character set and near the common ancestor, can improve resolution of a phylogeny. This is caused by improved knowledge of ancestral characters, constraining the possible inferred states at internal nodes of the cladogram, thereby reducing the number of most parsimonious trees in phylogenetic analysis. A fully reconstructed 48 million-year-old fossil *Decodon* is clearly closer to the common ancestor of the clade than any living species, thereby fulfilling both of Huelsenbeck's criteria for when fossils are more valuable than extant taxa in phylogenetic analysis. As not all intrafamilial relationships in Lythraceae are well supported in both morphological and molecular cladistic analyses (Graham et al., 1993; Conti et al., 1997; Shi et al., 2000; Huang and Shi, 2002), the importance of a complete character set for a fully reconstructed and anatomically preserved fossil plant is highlighted. Therefore, the Princeton chert has great value, not only providing in depth knowledge of an ancient biota (Cevallos-Ferriz et al., 1991; Pigg and Stockey, 1996), but also towards elucidating uncertain phylogenetic hypotheses through detailed anatomical character sets, including those from reconstructed fossil plants.

## LITERATURE CITED

ALVIN, K. L., AND M. C. BOULTER. 1974. A controlled method of comparative study of taxodiaceous leaf cuticles. *Botanical Journal of the Linnean Society* 69: 277–286.

AMARASINGHE, V., S. A. GRAHAM, AND A. GRAHAM. 1991. Trichome morphology in the genus *Cuphea* (Lythraceae). *Botanical Gazette* 152: 77–90.

BASINGER, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 59: 2379–2410.

BASINGER, J. F., AND G. W. ROTHWELL. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 55: 1984–1990.

CEVALLOS-FERRIZ, S. R. S., AND R. A. STOCKEY. 1988. Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Lythraceae. *Canadian Journal of Botany* 66: 303–312.

CEVALLOS-FERRIZ, S. R. S. AND R. A. STOCKEY. 1989. Permineralized fruits and seeds from the Princeton Chert (Middle Eocene) of British Columbia – Nymphaeaceae. *Botanical Gazette* 150: 207-217.

CEVALLOS-FERRIZ, S. R. S., R. A. STOCKEY, AND K. B. Pigg. 1991. The Princeton chert: evidence for in situ aquatic plants. *Review of Palaeobotany and Palynology* 70: 173–185.

CHANDLER M. E. J. 1961. Flora of the Lower Headon Beds of Hampshire and the Isle of Wight. *Bulletin of the British Museum (Natural History) Geology* 5: 93–157.

CONTI, E., A. LITT, AND K. J. SYTSMA. 1996. Circumscription of Myrtales and their relationships to other rosids: evidence from *rbcL* sequence data. *American Journal of Botany* 83: 221– 233.

CONTI, E., A. LITT, P. G. WILSON, S. A. GRAHAM, B. G. BRIGGS, L. A. S. JOHNSON, AND K. J. SYTSMA. 1997. Interfamilial relationships in Myrtales: Molecular phylogeny and patterns of morphological evolution. *Systematic Botany* 22: 629–647.

CURRAH, R. S. AND R. A. STOCKEY. 1991. A fossil smut fungus from the anthers of an Eocene angiosperm. *Nature* 350: 698–699.

DAHLGREN, R., AND R. F. THORNE. 1984. The Order Myrtales: circumscription, variation, and relationships. *Annals of the Missouri Botanical Garden* 71: 633–699.

FRIIS, E. M. 1985. Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark). *Biologiske Skrifter, Det Kongelige Danske Videnskabernes Selskab* 24: 1–165.

GIN, A. 1909. Recherches sur les Lythracées. *Travaux du Laboratoire de Matière Médicale de l'Ecole Superieure de Pharmacie de Paris* 6(3): 1–168.

GRAHAM, S. A. 1964. The genera of Lythraceae in the southeastern United States. *Journal of the Arnold Arboretum* 45: 235–251.

GRAHAM, S. A. 1999. The emerging picture of Lythraceae: cladistic analysis of morphological and cpDNA characters. *XVI International Botanical Congress Abstracts* p. 250.

GRAHAM, A., AND S. A. GRAHAM. 1971. The geologic history of the Lythraceae. *Brittonia* 23: 335–346.

GRAHAM, S. A., J. V. CRISCI, AND P. C. HOCH. 1993. Cladistic analysis of the Lythraceae sensu lato based on morphological characters. *Botanical Journal of the Linnean Society* 113: 1–33.

GRAHAM, S. A., R. F. THORNE, AND J. L. REVEAL. 1998. Validation of subfamily names in *Lythraceae*. *Taxon* 47: 435–436.

HILLS, L. V., AND H. BAADSGAARD. 1967. Potassium-argon dating of some lower Tertiary strata in British Columbia. *Canadian Petroleum Geology* 15: 138–149.

HUANG, Y., AND S. SHI. 2002. Phylogenetics of Lythraceae sensu lato: a preliminary analysis based on chloroplast *rbcL* gene, *psaA-ycf3* spacer, and nuclear rDNA internal transcribed spacer (ITS) sequences. *International Journal of Plant Sciences* 163: 215–225.

HUELSENBECK, J. P. 1991. When are fossils better than extant taxa in phylogenetic analyis? *Systematic Zoology* 40: 45-469.

JAYAWEERA, M. A. 1967. The genus *Duabanga*. *Journal of the Arnold Arboretum* 48: 89–100.

JOHANSEN, D. A. 1940. Plant microtechnique. McGraw–Hill Book Company, Inc., New York, New York, USA.

JOHNSON L. A. S., AND B. G. BRIGGS 1984. Myrtales and Myrtaceae a phylogenetic analysis. *Annals of the Missouri Botanical Garden* 71: 700-756.

JOY, K. W., A. J. WILLIS, AND W. S. LACEY. 1956. A rapid cellulose peel technique in paleobotany. *Annals of Botany (London), new series* 20: 635–637.

JUDD, W. S., C. S. CAMPBELL, E. A. KELLOGG, AND P. F. STEVENS. 1999. Plant systematics: a phylogenetic approach. Sinauer Associates, Inc., Sunderland, Massachusetts, U.S.A.

KEATING, R. C. 1982. The evolution and systematics of Onagraceae: leaf anatomy. *Annals of the Missouri Botanical Garden* 69: 770–803.

KEATING, R. C. 1984. Leaf histology and its contribution to relationships in the Myrtales. *Annals of the Missouri Botanical Garden* 71: 801–823.

KOEHNE, E. 1903. Lythraceae. *In* A. Engler [ed.], Das Pflanzenreich, Heft 17. IV 216: 1–326. Englemann, Leipzig, Germany.

KVAČEK, Z., AND J. SAKALA. 1999. Twig with attached leaves, fruits and seeds of *Decodon* (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds. *Review of Palaeobotany and Palynology* 107: 201–222.

LITTLE, S. A., AND R. A. STOCKEY. 2003. Vegetative growth of *Decodon allenbyensis* (Lythraceae) from the Middle Eocene Princeton chert with anatomical comparisons to *D. verticillatus*. *International Journal of Plant Sciences* 164: 453–469.

MANCHESTER, S. R., D. L. DILCHER, AND S. L. WING. 1998. Attached leaves and fruits of myrtaceous affinity from the Middle Eocene of Colorado. *Review of Palaeobotany and Palynology* 102: 153–163.

METCALFE, C. R., AND L. CHALK. 1950. Anatomy of the Dicotyledons, vols. I & II. Oxford University Press, Oxford, UK.

MUJICA, M. B., AND D. F. CUTLER. 1974. Taxonomic implications of anatomical studies on the Oliniaceae. *Kew Bulletin*. 29: 93–123.

MULLER, J. 1981. Fossil pollen records of extant angiosperms. *The Botanical Review* 47: 1–142.

PIGG, K. B., AND R. A. STOCKEY. 1996. The significance of the Princeton chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. *Washington Geology* 24: 32–36.

PIGG, K. B., R. A. STOCKEY, AND S. L. MAXWELL. 1993. *Paleomyrtinaea* a new genus of permineralized myrtaceous fruits and seeds from the Eocene of British Columbia and Paleocene of North Dakota. *Canadian Journal of Botany* 71: 1–9.

REID, E. M., AND M. E. J. CHANDLER. 1933. The London Clay flora. British Museum (Natural History) London, UK.

ROBISON, C. R., AND C. P. PERSON. 1973. A silicified semiaquatic dicotyledon from the Eocene Allenby Formation of British Columbia. *Canadian Journal of Botany* 51: 1373-1377.

RODRÍGUEZ-DE LA ROSA, R. A., S. R. S. CEVALLOS-FERRIZ, AND A. SILVA-PINEDA. 1998. Paleobiological implications of Campanian coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 142: 231–254.

RAO, T. A., and S. DAS. 1979. Leaf sclereids – occurrence and distribution in the angiosperms. *Botaniska Notiser* 132: 319–324.

SHI, S., Y. HUANG, F. TAN, X. HE, AND D. E. BOUFFORD. 2000. Phylogenetic analysis of the Sonneratiaceae and its relationship to Lythraceae based on ITS sequences of nrDNA. *Journal of Plant Research* 113: 253–258.

SMITH, S. Y. AND R. A. STOCKEY. 2003. Aroid seeds from the Middle Eocene Princeton chert (*Keratosperma allenbyense*, Araceae): Comparisons with extant Lasioideae. *International Journal of Plant Sciences* 164: 239–250.

SOLEREDER, H. 1908. Systematic anatomy of the Dicotyledons, vols. I & II. Clarendon Press, Oxford.

STOCKEY, R. A., AND K. B. PIGG. 1994. Vegetative growth of *Eorhiza arnoldii* Robison and Person from the Middle Eocene Princeton chert locality of British Columbia. *International Journal of Plant Sciences* 155: 606–616.

STOCKEY, R. A., AND W. C. WEHR. 1996. Flowering plants in and around Eocene lakes of the interior. *In*: Rolf Ludvigsen [ed.] Life in stone: A natural history of British Columbia's fossils, Pages 234–247. University of British Columbia Press, Vancouver, British Columbia, Canada.

THORNE, R. F. 1992a. Classification and geography of the flowering plants. *The Botanical Review* 58: 225–348.

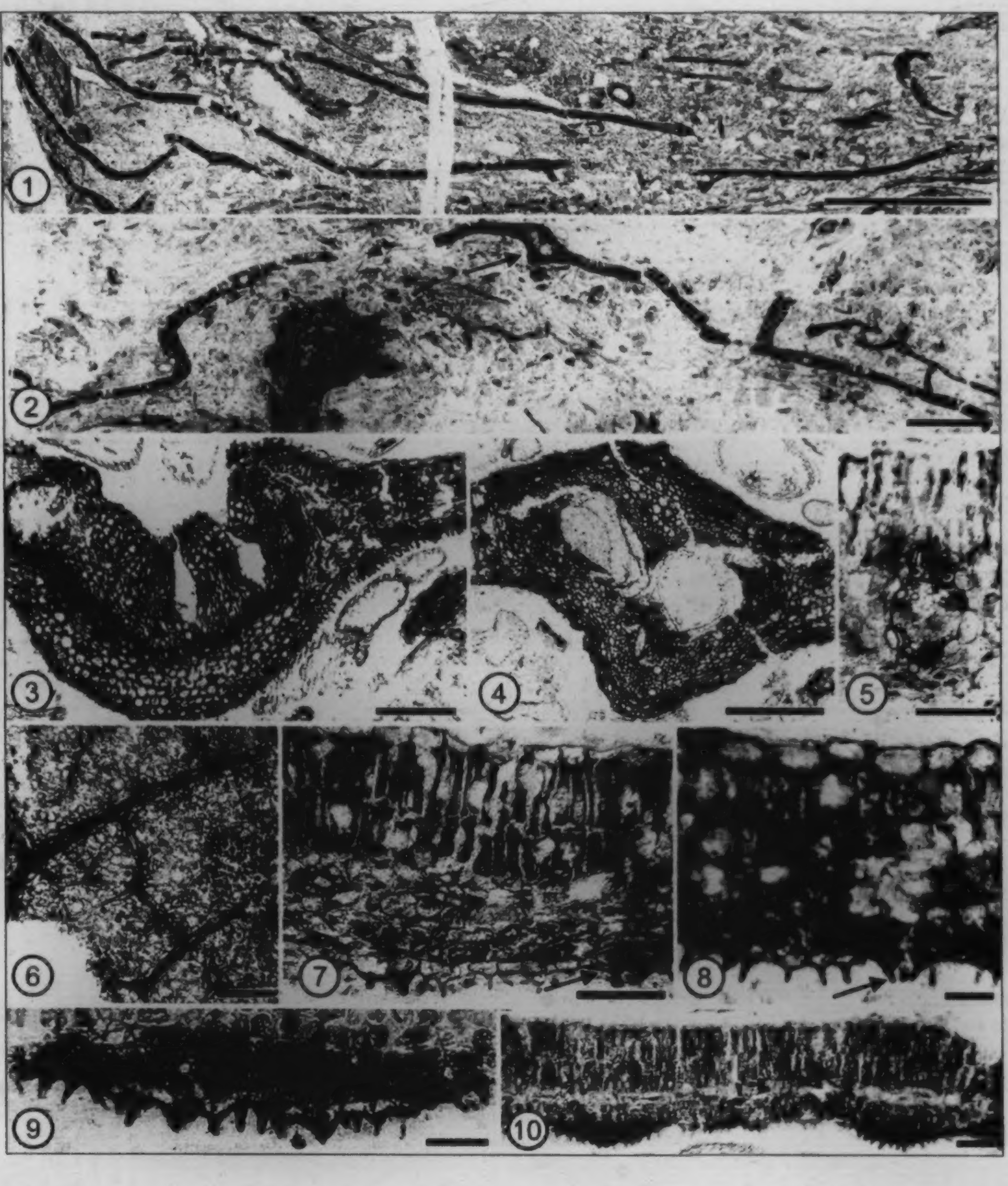
THORNE, R. F. 1992b. An updated phylogenetic classification of the flowering plants. *Aliso* 13: 365–389.

TIFFNEY, B. H. 1981. Fruits and seeds of the Brandon Lignite, VI. *Microdiptera* (Lythraceae). *Journal of the Arnold Arboretum* 62: 487–513.

WEHR, W. C., AND D. Q. HOPKINS. 1994. The Eocene orchards and gardens of Republic, Washington. *Washington Geology* 22: 27–34.

WOLFE, J. A., and T. TANAI. 1980. The Miocene Seldovia Point flora of the Kenai Group, Alaska. *United States Geological Survey Professional Paper* 1105: 1–52.

**Figs. 4.1–4.10**. Light micrographs of sections of fossil lythraceous leaves. **4.1.** Transverse sections of several leaves in chert matrix. P5104 C top #2. Bar = 5 mm. **4.2.** Transverse section of leaf with midrib (arrow) and lamina. P5999 D #4. Bar = 2 mm. **4.3.** Transverse section of leaf midrib showing vascular tissues, presence of papillate abaxial epidermis over lamina, and absence of papillae over midrib. P5139 D bot #2a. Bar = 0.2 mm. **4.4.** Transverse section of leaf midrib showing continuity of tissues on adaxial surface P5999 D #4. Bar = 0.3 mm. **4.5.** Transverse section of leaf showing vascular bundle with bundle sheath. P4947 B bot #9a. Bar = 0.06 mm. **4.6.** Paradermal section through mesophyll, showing veins. P4947 B bot #3a. Bar = 0.2 mm. **4.7.** Transverse section of leaf showing abaxial epidermis, double palisade, spongy mesophyll, and abaxial epidermal papillae surrounding possible stoma (arrow). P5997 D top #2. Bar = 0.05mm. **4.8.** Abaxial epidermis showing papillae surrounding possible stoma (arrow). P5139 D bot #2a. Bar = 0.04 mm. **4.9.** Leaf abaxial surface showing fungal stroma beneath and invading epidermal papillae. P5997 D top #11. Bar = 0.04 mm. **4.10.** Leaf with abaxial fungal infection. P5981 C #1. Bar = 0.1 mm.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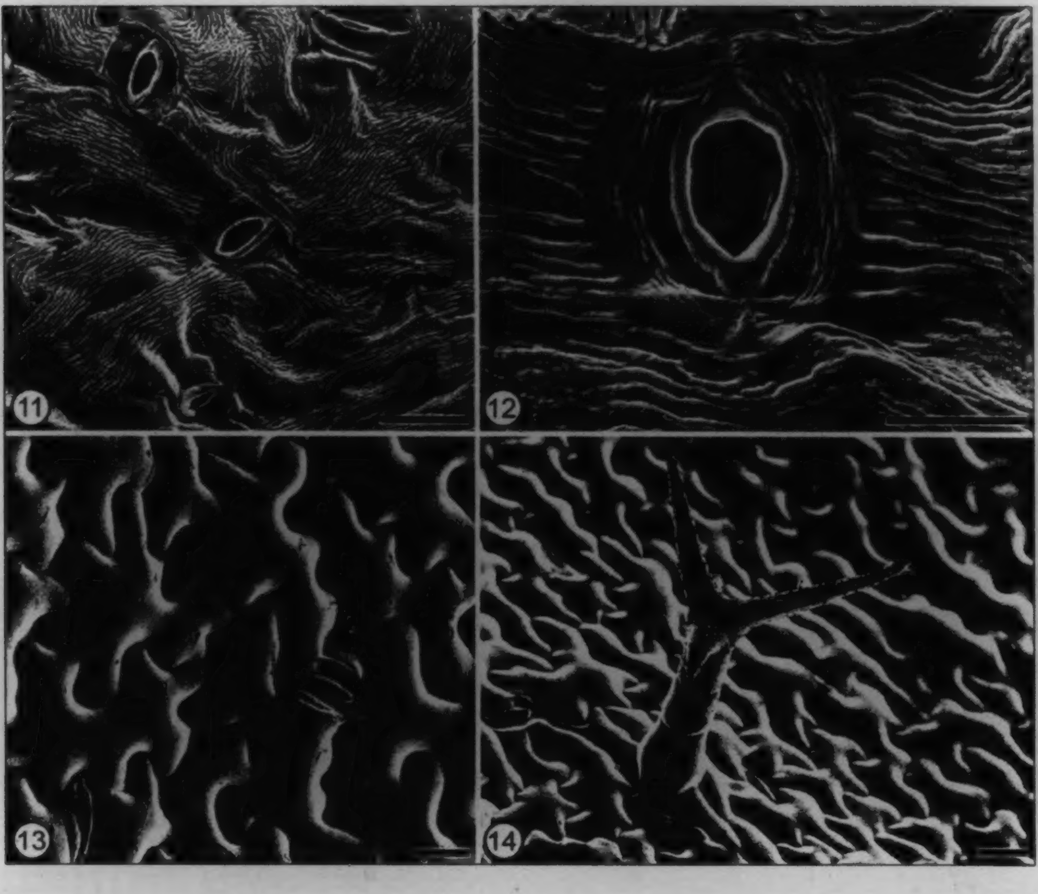
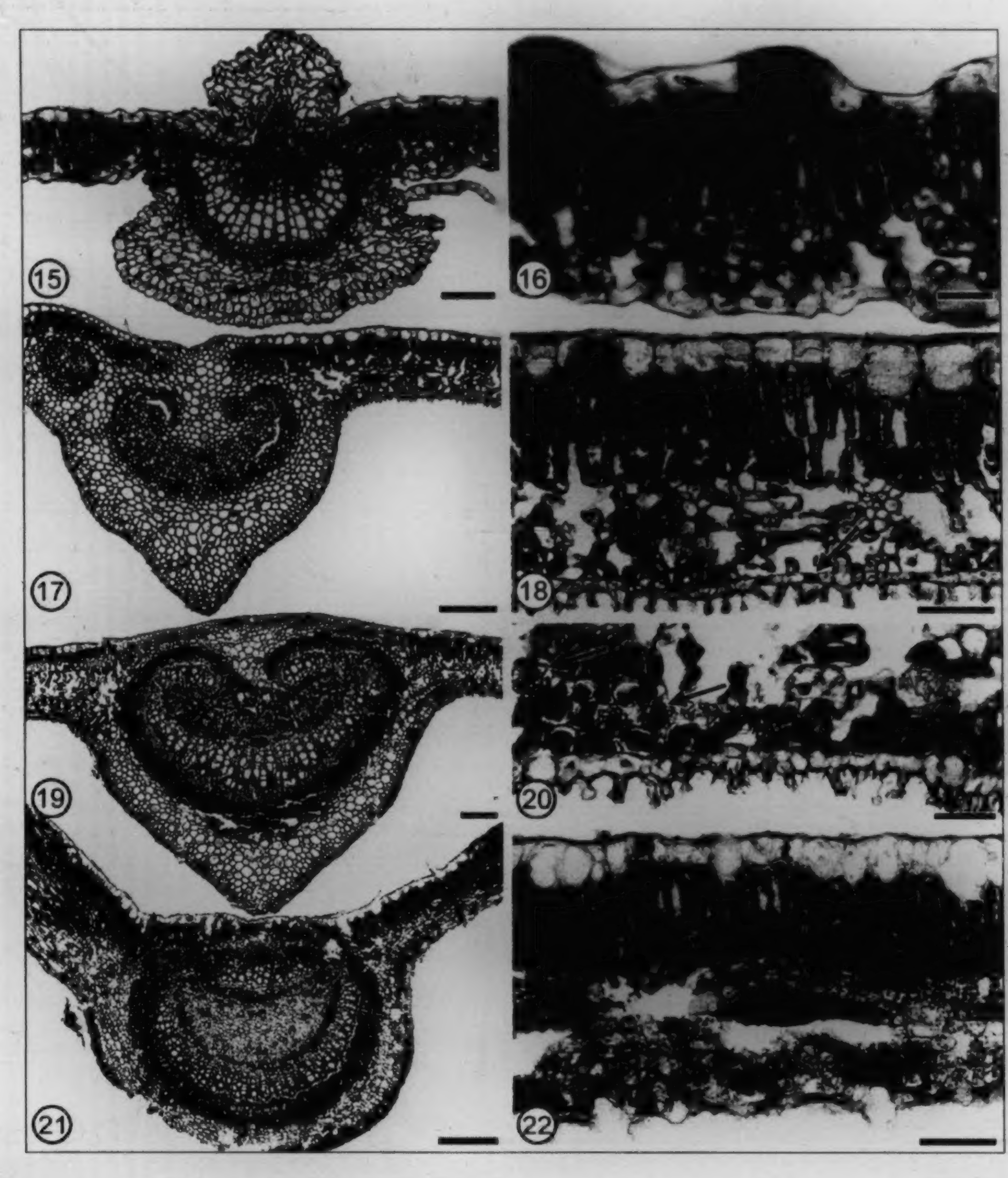
**Figs. 4.11–4.14**. Scanning electron microscopy of *Decodon verticillatus* leaves. **4.11.** Adaxial cuticle showing stomata after chromium trioxide technique and air drying. Decolf13. Bar = 0.02 mm. **4.12.** Adaxial cuticle on stomatal apparatus after chromium trioxide technique, showing striations. Decolf13. Bar = 0.01 mm. **4.13.** External abaxial leaf surface under Cryo-SEM showing anomocytic stomata. Decryl02. Bar = 0.02 mm. **4.14.** External abaxial leaf surface under Cryo-SEM showing numerous trichomes over vein. Decryl03. Bar = 0.10 mm.

Figs. 4.11–4.14

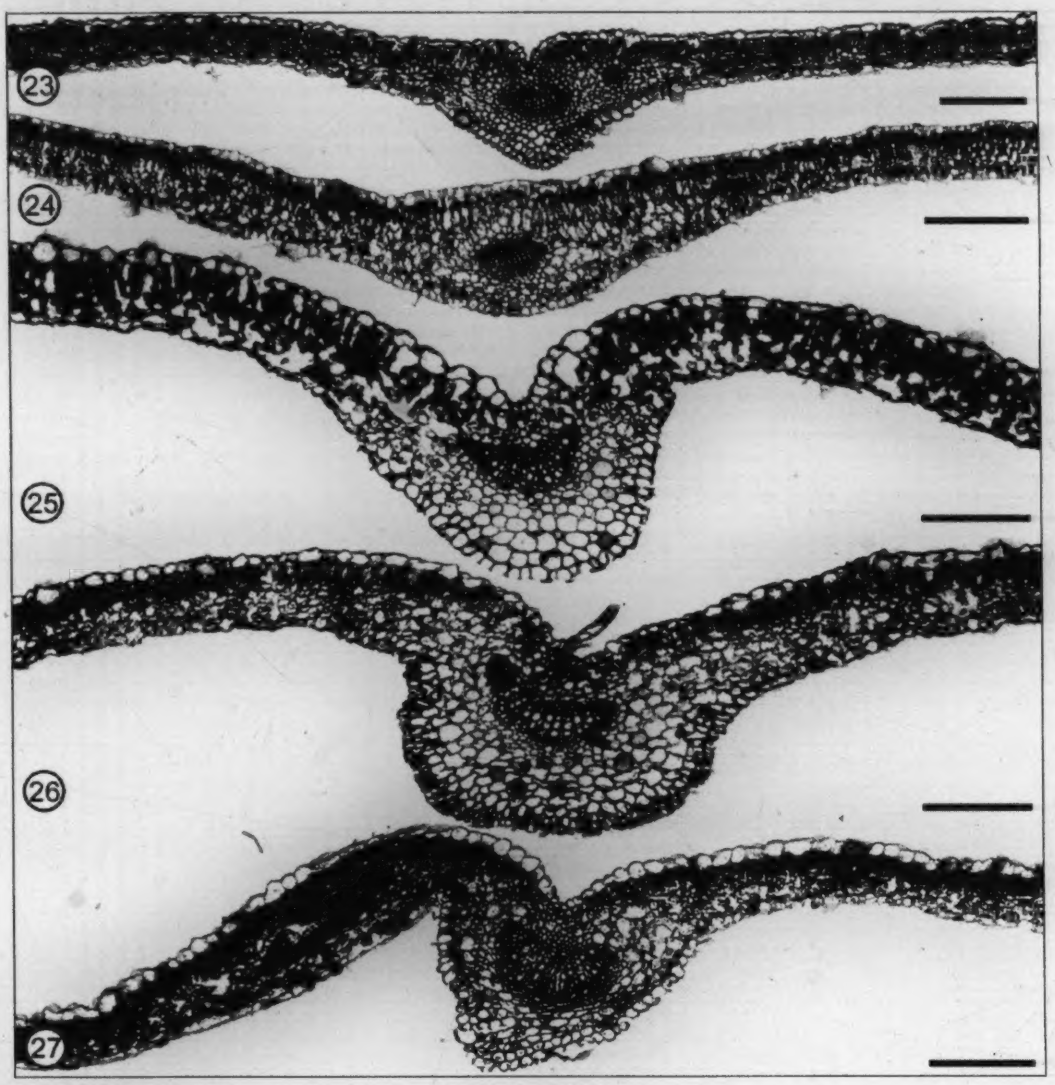


**Figs. 4.15–4.22.** Light micrographs of transverse sections of leaves of Lythraceae (Lythroideae and Duabangoideae). **4.15.** *Decodon verticillatus* (L.) Ell. showing adaxial midrib bulge, C-shaped xylem strand, double palisade, and multicellular trichome, at right. SL12902. Bar = 0.1 mm. **4.16.** *D. verticillatus* lamina showing double palisade and enlarged mucilage cells in epidermis. SL12902. Bar = 0.03 mm. **4.17.** *Duabanga grandiflora* (Roxb. ex DC) Walpers showing C-shaped midvein and trace to secondary vein with flat to slightly grooved adaxial surface and prominent ridged abaxial surface. 2062 #1. Bar = 0.3 mm. **4.18.** *Duabanga grandiflora* lamina showing double palisade, adaxial epidermis with mucilage cell, and abaxial epidermal papillae overarching stoma (arrow). 1859 #1. Bar = 0.1 mm. **4.19.** *Duabanga grandiflora* showing strongly curved midvein, nearly flattened adaxial surface, and prominent ridge on abaxial surface. 1859 #1. Bar = 0.3 mm. **4.20.** *Duabanga grandiflora* lamina showing spongy mesophyll with druses (arrows) and finely ornamented, abaxial, epidermal papillae. 1859 #1. Bar = 0.05 mm. **4.21.** *Duabanga moluccana* Bl. Showing broad flat zone of adaxial midrib, circular midvein, and prominent rounded abaxial midrib. 1935 #4. Bar = 0.3 mm. **22.** *Duabanga moluccana* lamina showing double palisade, epidermal mucilage cells, and lack of abaxial papillae. 1935 #4. Bar = 0.1 mm.

Figs. 4.15–4.22



**Figs. 4.23–4.27**. Light micrographs of transverse sections of leaves of Lythraceae (Lythroideae). **4.23.** *Lythrum alatum* var. *lanceolatum* (Ell.) Rothrock showing adaxial groove and epidermal mucilage cells. 1729 #1. Bar = 0.2 mm. **4.24.** *Nesaea longipes* A. Gray showing smooth adaxial surface and epidermal mucilage cells. 1727 #4. Bar = 0.3 mm. **4.25.** *Ammannia coccinea* Rottb. showing grooves adaxial surface and mucilage cells in adaxial epidermis. 2126 #1. Bar = 0.2 mm. **4.26** *Cuphea spectabilis* S. Graham showing adaxial groove, mucilage cells, and multicellular trichome. 1726 #1. Bar = 0.2 mm. **4.27** *Heimia salicifolia* (H.B.K.) Link. showing adaxial groove and mucilage cells. 1728 #2. Bar = 0.2 mm.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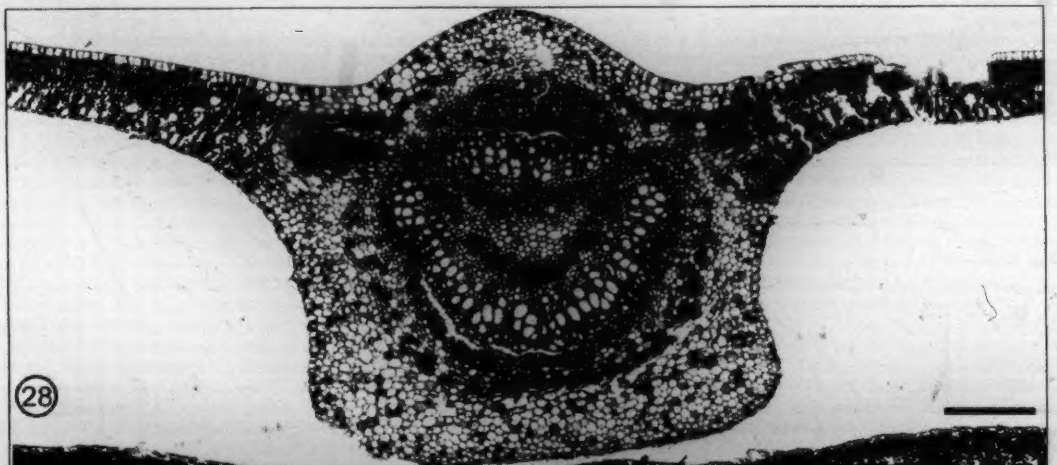
**Figs. 4.28–4.30.** Light micrographs of transverse sections of leaves of Lythraceae (Lythroideae). **4.28.** *Lagerstroemia speciosa* (L.) Pers. showing nearly cylindrical midvein with adaxial ridge prominent abaxial bulge with angular outline. 1794 #2. Bar = 0.3 mm. **4.29.** *Lafoensia speciosa* (H.B.K.) DC showing C-shaped midvein and grooved adaxial surface. 1784 #1. ×57. Bar = 0.2 mm. **4.30.** *Lawsonia inermis* L. showing nearly circular midrib with C-shaped vein and epidermal mucilage cells. 1808 #2. Bar = 0.2 mm.



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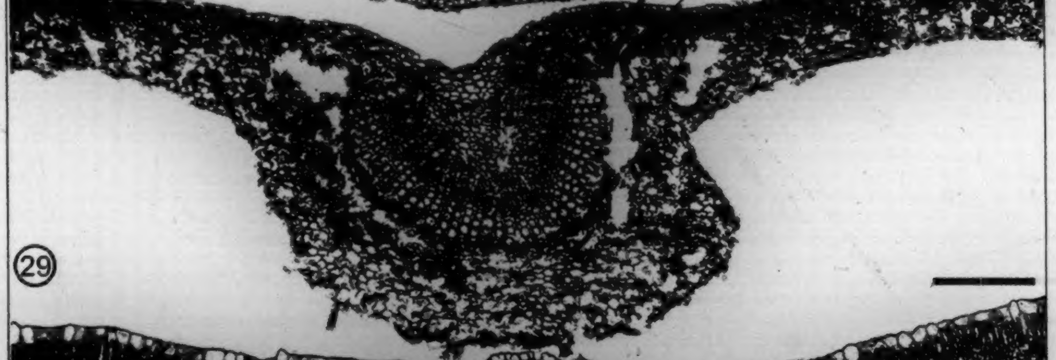

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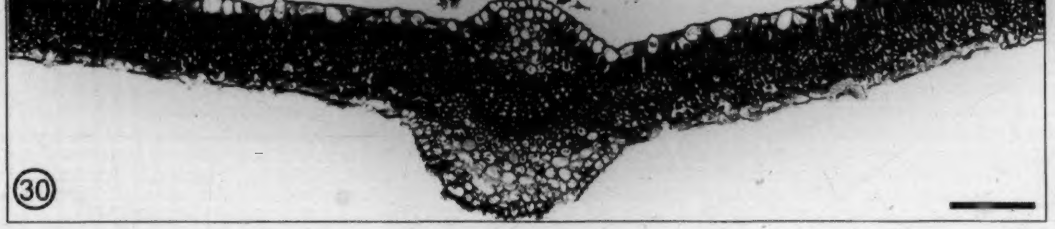

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**Figs. 4.31–4.34.** Light micrographs of transverse sections of leaves of Lythraceae (Punicoideae and Sonneratioideae). **4.31.** *Punica protopunica* Balf. f. showing small C-shaped midvein, level adaxial surface, and slightly convex abaxial surface of midrib. C2180 #2. Bar = 0.2 mm. **4.32.** *Punica granatum* L. showing slightly grooved adaxial surface, C-shaped midvein, and rounded, convex abaxial surface. 1810 #1. Bar = 0.1 mm. **4.33.** *Sonneratia* sp. showing nearly flat adaxial midrib, C-shaped midvein, slightly ridged abaxial midrib, and epidermal mucilage cells. 1892 #2. Bar = 0.3 mm. **4.34.** *Sonneratia apetala* Buch.-Ham. showing isobilateral leaf with two zones of palisade, oval-shaped midvein with gently sloping midrib. 1926 #4. Bar = 0.3 mm.

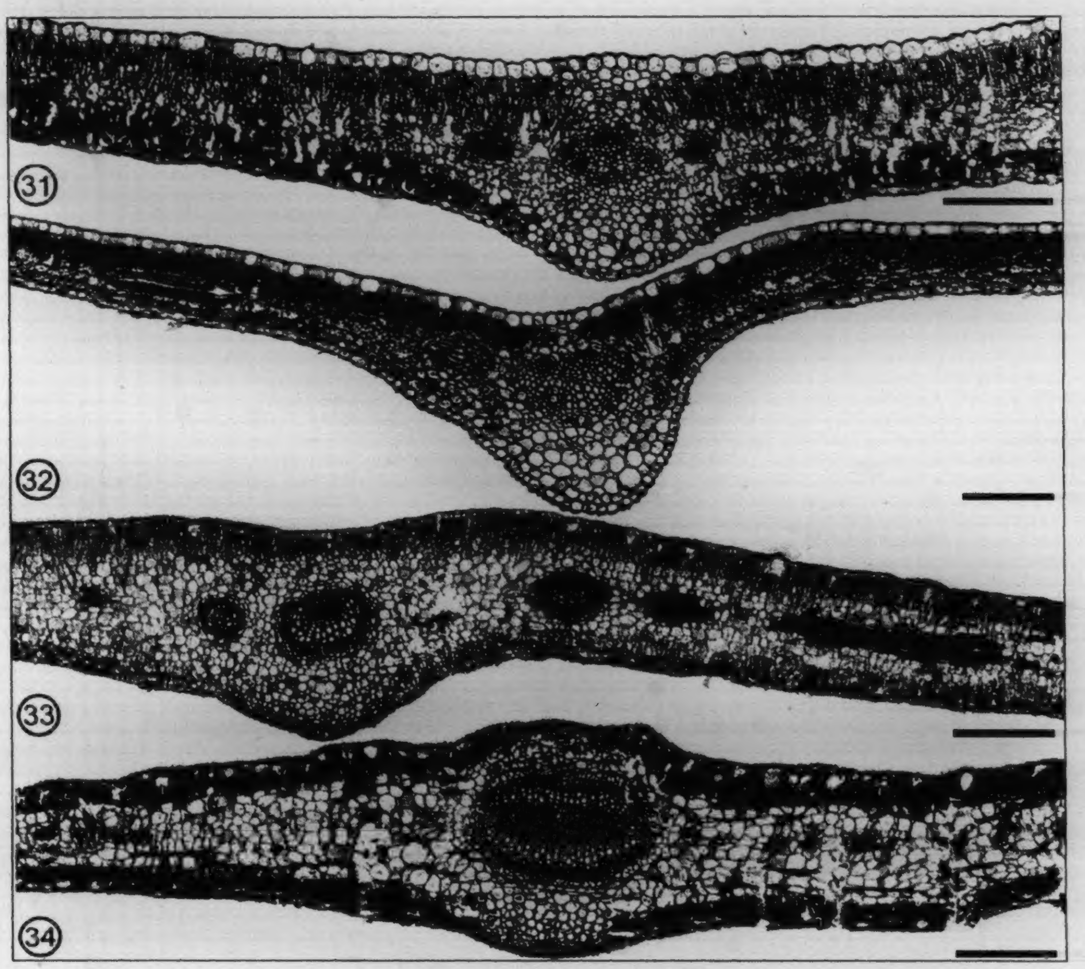
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TABLE 4.1. Selected anatomical features for leaves of Lythraceae. Characters in boldface type match or overlap with those [illegible] fossil leaf.

| | Midvein | | | | Secondary veins | | | | | Mesophyll | | | | | | Epidermis | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Rib[a] | | Vein | | Rib[a] | | Vein | | | | | | | | | Cells | | | | | Stomata | |
| Species | External adaxial shape | External abaxial shape | Shape x.s.[b] | Fibers[d] | External adaxial shape | External abaxial shape | Shape x.s.[c] | Fibers[d] | Adaxial extension | Structure[e] | No. palisade layers | Lamina palisade (%) | No. spongy layers | Sclereids | Crystals[f] | Size[g] | Papillate abaxial cells | Mucilage cells[h] | Birefringent crystals | Trichomes[*] | Stomatal location[i] | Stomata level[j] |
| Fossil leaf | Co | Co-V | si | SX | Co-Fl | Co | c | S | – | D | 2(–3) | 30 | 5–7 | – | ? | ad > ab | + | ? | ? | – | Ab | l |
| *Decodon verticillatus* | Co | Tr | s | — | Co | Tr | a | — | – | D | 1 | 50 | 3 | – | D | = | – | E | + | + | Am | l |
| *Duabanga grandiflora* | Ca-Fl-Co | V | si | SX | Co-Fl | Co | c | S | – | D | 2(–3) | 40–50 | 4–9 | – | D | ad > ab | + | E | – | – | Ab | l |
| *Duabanga moluccana* | Co-Fl | Co-Sq | cy | AdI | Fl | Co | c | S | + | D | 2(–3) | 40–50 | 4–6 | – | D | ad > ab | – | E | – | – | Am, Ab | l&s |
| *Lythrum alatum* | Co | V | a | — | Co | Co | ci | — | – | D | 1(–2) | 30 | 3 | – | D | = | – | E | + | – | Am | l |
| *Nesaea longipes* | Co-Fl | Co | s | — | Co | Co | ci | — | – | D | 1 | 30 | 5 | – | D | = | – | E | – | – | Am | l |
| *Ammannia coccinea* | Ca | Co | s | — | Fl | Fl | ci | — | – | D | 1 | 50 | 3–5 | – | D | ad > ab | – | E | + | – | Am | l |
| *Cuphea spectabilis* | Ca | Co-Sq | a | — | Ca | Co | a | — | – | D | 1 | 30 | 5 | – | D | ad > ab | – | E | – | + | Am | l |
| *Heimia salicifolia* | Ca | V | a | — | Co | Co | a | — | – | D | 1 | 30 | 3–5 | – | D | = | – | E | – | – | Ab | l |
| *Lagerstoemia speciosa* | Co | Sq | cy | S | Fl | Co | a | AbB | + | D | 2 | 40 | 4–6 | – | D, P | ad > ab | – | E | + | – | Ab | l |
| *Lafoensia speciosa* | Co | Sq | s | AbB | Fl | Co | a | AbB | + | D | 1 | 25 | 6–8 | – | D, P | = | – | E | + | – | Ab | l |
| *Lawsonia inermis* | Co | Co | a | — | Fl | Fl | ci | — | – | D | 1(–2) | 30–40 | 4–6 | – | D | ad > ab | – | E | – | – | Am | l |
| *Punica protopunica* | Co-Fl | Co | a | — | Co-Fl | Co | a | — | + | D-I | 2(–3) | 30–40 | 5–8 | – | D, P | ad > ab | – | — | – | – | Ab | l |
| *Punica granatum* | Ca-Fl | Co | a | — | Fl | Co | a-ci | — | – | D | 1 | 40–50 | 3–4 | – | D, P | ad > ab | – | — | – | – | Ab | l |
| *Sonneratia sp.* | Ca-Fl | Co | s | — | Fl | Fl | c | — | – | D-I | 3(–4) | 25–30 | 10–12 | + | D | = | – | M | – | – | Am | s |
| *Sonneratia apetala* | Co | Co | cy | — | Fl | Fl | c | — | – | I | 3 + 3 | 50–60 | 5–8 | + | D | = | – | M | – | – | Am | s |

[a] Rib shape: Co = convex; Ca = concave; Fl = flat; Sq = square; Tr = trapezoidal; V = V-shaped.

[b] Midvein shape: s = C-shaped; si = C-shaped with incurved abaxial ends; cy = cylinder.

[c] Secondary vein shape: c = C-shaped; a = weak arc; ci = circular.

[d] Vein fibers: SX = surround midvein except for adaxial gap; S = surround midvein; AdI = adaxial and lateral islands of fibers; AbB = abaxial band.

[e] Structure: D = dorsiventral; I = isobilateral.

[f] Crystals: D = druses; P = prismatics.

[g] Size: ad > ab = adaxial epidermal cells larger than abaxial; ad = ab = adaxial epidermal cells similar in size to abaxial.

[h] Mucilage cells: E = mucilage cells are epidermal; M = mucilage cells in mesophyll/below epidermis.

[*] Trichomes: presence or absence scored here, but Lythraceae trichome types are diverse and taxonomically important (Koehne, 1881; Amarasinghe et al., 1991).

[i] Stomatal location: Ab = Abaxial stomata only; Am = Amphistomatic/stomata adaxial and abaxial.

[j] Stomata level: l = guard cells level with epidermis, s = guard cells sunken into epidermis.

## Appendix: Index of specimens shown in the plates.

*Decodon verticillatus* (L.) Ell. SL12902 = S.A.Graham 578; Portage Co., Wingfoot Lake, OH.

*Duabanga grandiflora* (Roxb. ex DC) Walpers 2062#1 = C1613 (as *D. sonneratoides*, a synonym).

*Duabanga grandiflora* 1859#1 = C1501; B.C.Stone 12837; U. Malaya; Perak, Malaya.

*Duabanga moluccana* Bl. 1935#4 = C1540; L.Madani; SAN 81066; Sepilok Forest Reserve; Sandakan, Sabah.

*Lythrum alatum var lanceolatum* (Ell.) Rothrock 1729 #1 = C1300; S.A. Graham 460 (MICH) ; Rankin Co., MS.

*Nesaea longipes* A Gray 1727#4 = C1298; B.L.Turner 6163 (TEX) (progeny), Mexico: Coahuila.

*Ammannia coccinea* Rottb. 2126#1 = C1669; S.Graham 489 (MICH) (progeny); Grayson Co., TX.

*Cuphea spectabilis* S. Graham 1726#1 = C1297; J.Reveal, et al. 4339 (MARY); (progeny) Mexico: Guerrero.

*Heimia salicifolia* (H.B.K.) Link. 1728#2 = C1299; S.A.Graham 141 (MICH); (progeny); Mexico: Jalisco.

*Lagerstroemia speciosa* (L.) Pers. 1794#2 = C1445; (obtained by P.H.Raven; cult FTG (Fairchild Tropical Garden), 57-119).

*Lafoensia speciosa* (H.B.K.) DC 1784#1 = C1433; (obtained by P.H.Raven; cult FTG, X-5-20).

*Lawsonia inermis L.* 1808#2 = C1461; P.H.Raven 26570; cult MO 751624-4; seed progeny; Hong Kong herbarium.

*Punica protopunica* Balf. f. C2180#2; P.Rudall, Jodrell Laboratory, cult K [also described as genus *Socotrea*, the second genus of Punicaceae, endemic to Socotra.

*Punica granatum* L. 1810#1 = C1463; P.H.Raven 26569; cult MO, source unknown.

*Sonneratia* sp. 1892#2 = C1563; B.C.Stone & E.F.Anderson BCS13165; = SAN86792; Sabah, Malaya.

*Sonneratia apetala* Buch.-Ham. 1926#4 = C1530; Thanikaimoni, s.n. 15mar77; Pichaveram mangrove; Pondicherry, India.

# CHAPTER 5

## *Similkameena borealis* gen. et sp. nov. (Lauraceae), flowers and inflorescences

### INTRODUCTION

Lauraceae is a large family with approximately 50 genera and 2500-3000 species distributed in the tropics, subtropics and parts of temperate regions (Meissner 1864; Pax 1891; Kostermans 1957; Hutchinson 1964, Rohwer 1993, 1999). Recent molecular phylogenetic studies have improved resolution of intrafamilial relationships (Rohwer 2000; Chanderbali et al. 2001; Rohwer and Rudolph 2005). However, it remains difficult to identify plants to species or genera (Kostermans 1957; van der Werff and Richter 1996) causing tests of evolutionary hypotheses in Lauraceae to be challenging. Recognizing natural phylogenetic groups, is difficult even in the context of molecular phylogenies, where several genera are clearly polyphyletic (Rohwer 2000; Chanderbali et al. 2001; Li et al. 2004, Rohwer and Rudolph 2005). However, within Order Laurales, both molecular (Renner 1998, 1999; Rohwer 2000; Chanderbali et al. 2001; Rohwer and Rudolph 2005) and morphological studies (Rohwer 1993) suggest Lauraceae to be monophyletic.

Lauraceae typically share a suite of characters that includes a woody habit (excluding parasitic *Cassytha* L.), small trimerous flowers, a perianth of tepals in two whorls and an androecium with three fertile whorls and a fourth innermost staminodal whorl (Rohwer 1993, Eklund 1999). In addition, Lauraceae usually have bi- or tetrasporangiate anthers that dehisce by valves, paired glandular appendages on filaments in the third androecial whorl, and a unilocular, unicarpellate gynoecium containing a single, apical, anatropous ovule (Boyle 1980; Heo et al. 1998). Exceptions or variations in this syndrome of floral characters are often used to define genera or species (Kostermans 1957; Rohwer 1993). Variations in inflorescence architecture are known in extant Lauraceae, and include paniculate, racemose, pseudo-umbellate types, as well as inflorescences reduced to single flowers (Weberling 1985; van der Werff and Richter 1996; van der Werff 2001).

Fossils of Lauraceae are often limited to megafossils, and occur from the mid-Cretaceous (Drinnan et al. 1990) to the Neogene (Eklund 1999). Approximately 40 genera and more than 500 lauraceous species have been reported from the Early Cretaceous to the Neogene (Eklund 2000). Fossil taxa, based on vegetative organs such as leaf compressions or wood, are difficult or impossible to assign unequivocally to Lauraceae, or to genera within Lauraceae (Kostermans 1957; Ferguson 1974; Eklund 2000; Li and Christophel 2000), whereas fruits and flowers, which have more diagnostic characters, are more easily placed in Lauraceae. Fossil pollen of Lauraceae is largely missing from the fossil record (Müller 1981), and is considered poorly suited for preservation due to low pollen production and the presence of a thin, discontinuous, or absent exine, which does not survive well after acetolysis (MacPhail 1980; Müller 1981). However, fossil lauraceous pollen has been reported in, or on, several fossil flowers, including *Perseanthus* Herendeen, Crepet et Nixon (1994), *Neusinia* Eklund (2000), and *Androglandula* Taylor (1988).

Few fossil lauraceous flowers are known from the Paleogene (Eklund, 2000), and only one species, based on flower compressions, is known from the Paleogene of North America (Taylor 1988). The current study describes an extinct Eocene lauraceous taxon based on flowers and inflorescences from the Princeton Chert (Allenby Formation) of British Columbia (Sun and Stockey 1991). *Similkameena borealis* gen. et sp. nov. contributes to the growing knowledge of fossil Lauraceae. The numerous characters provided by immature, but complete, anatomically preserved, inflorescences, in bud, allow for detailed comparisons to known fossil flowers and to extant genera. *Similkameena borealis* represents the first anatomically preserved fossil floral remains of Lauraceae in the Paleogene of North America. Further, this genus is the only known fossil Lauraceae with determinate thyrsopaniculate inflorescences with cymose lateral axes.

## MATERIAL AND METHODS

The Princeton Chert locality is situated on the east bank of the Similkameen River, ca. 8.4 km southwest of the town of Princeton, British Columbia (UTM 10U FK 786725; 49° 22' 33" N, 120° 32' 18" W). The outcrop has also been called locality "I" (Boneham 1968) and is part of the Princeton Group, Allenby Formation. At least forty-nine interbedded layers of chert and coal occur, with occasional ash beds (Stockey 1983; Cevallos-Ferriz et al. 1991). Several of the chert layers split and anastomose, so that seventy separate chert layers are observed in some places along the 10 m high and 30 m long exposure (pers. observ. 2003). Differing plant associations are known among the chert layers (Pigg and Stockey 1996). Over 75 inflorescences are known and they occur in miscellaneous blocks (unknown layer #), but co-occur with remains of *Metasequoia milleri* Basinger et Rothwell. The locality is dated as Middle Eocene, based on data from pollen (Rouse and Srivastava 1970), fossil mammals (Russell 1935; Gazin 1953), fish (Wilson 1977, 1982), and potassium-argon dating (48.7 Ma) of ash layer #22 (Hills and Baadsgaard 1967; H. Baadsgaard, personal communication, 1999).

The permineralized plant remains occur in the chert blocks, which are collected in bulk, slabbed on an oil-cooled rock saw, and prepared using the cellulose-acetate peel technique (Joy et al. 1956) modified for hydrofluoric acid (Basinger and Rothwell 1977; Basinger 1981). All fossil specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Sections of consecutive peels were mounted with Eukitt rapid mounting medium (O. Kindler, GmbH, Freiburg, Germany) for light microscope examination. Images were taken with a Phase One digital scanning camera (Phase One A/S, Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe Photoshop. Characters were analyzed, in part, using the Delta Key program (Watson and Dallwitz 1992). Additionally, characters of inflorescences and flowers in extant genera were compiled for comparison to the fossil (Table 1). Data for Table 1 is mainly based on Kostermans (1957), Hyland (1989), and Rohwer (1993).

## SYSTEMATICS

Order: Laurales

Family: Lauraceae Juss.

Genus: *Similkameena* Little et Stockey gen. nov.

*Diagnosis*: Inflorescences thyrsopaniculate, lateral axes opposite, determinate/cymose. Lateral axes, and penultimate units of lateral axes enclosed by pubescent bracts. Flowers bisexual, actinomorphic. Terminal and penultimate flowers trimerous, with nine bilocular stamens in three whorls, staminodes absent. Basalmost flowers of lateral axes, dimerous with six bilocular stamens in three whorls, staminodes absent. Glandular appendages present near base of stamens in third whorl. Gynoecium unicarpellate, uniloculate, style short; ovule one, apical, anatropous. Trichomes, uniseriate, unbranched. Pith of inflorescence axis with sclereid clusters. Idioblasts present in all organs.

Species: *Similkameena borealis* Little et Stockey (Figs. 5.1-5.4)

*Diagnosis*: Inflorescences at least 4.5 mm long and 2.5 mm in diam, bearing at least 15-25 pedicellate flowers. Perianth of six tepals in two whorls in terminal and penultimate flowers of lateral axes; perianth of 4 tepals in two whorls in basalmost flowers of lateral axes. Stamens of outer two whorls introrse, innermost whorl extrorse; immature stamens with short filaments. Tepals sub-equal in immature flowers, inner tepals slightly smaller than outer. Receptacles wide, hypanthium shallow. Trichomes, abundant on bracts, few on tepals, absent from stamens, few around base of gynoecium. Sclereid clusters in pith of inflorescence axes; isolated sclereids present in bract midribs and mesophyll. Idioblasts, up to 70 μm in diam, present in all organs.

*Holotype*. P1332 B bot, $C_2$ top (Figs 5.1A; 5.2A, B; 5.3A, C, E; 5.4C): deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

*Paratypes*. P1060 $D_2$ bot, P1089 $C_2$ side, P1213 $D_2$ bot, P1237 $D_2$ bot, P1288 $C_2$

bot, P1312 $B_1$ top, P1349 C bot: deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

*Etymology*. The genus is named after the Similkameen River, where the Princeton Chert locality occurs. *Borealis* refers to the Northern Hemisphere occurrence of this fossil.

*Locality*. Princeton Chert locality, southern British Columbia, Canada (UTM 10U FK 786725; 49° 22' 33" N, 120° 32' 18" W)

*Stratigraphic occurrence*. Allenby Formation.

*Age*. Middle Eocene.

*Description*: Of the ca. 75 inflorescences, size is variable, as different stages of early development are present, and they are at least 4.5 mm long and at least 2.5 mm wide (Figs. 5.1; 5.2A, B). Inflorescence axes bear at least 15-25 flowers, and each ends in a terminal flower. Attached to the main axis are oppositely-arranged secondary axes, each subtended by a bract (Figs. 5.1; 5.2A, B). Each lateral axis bears a terminal flower, subtended by two oppositely-arranged penultimate flowers, each with a subtending pubescent bract (Figs. 5.1; 5.2A, B). Sometimes, small, immature, oppositely-arranged flowers are found below the penultimate flowers. In more mature axes, these small flowers are further developed, each with an enclosing bract. However, most inflorescences only show the three main flowers (i.e., single terminal flower, subtended by two oppositely arranged penultimate flowers) (Figs. 5.2A, B).

Each flower is pedicellate and bisexual, with pedicel length variable, depending on maturity (Fig. 5.4A). At the base, the flowers have shallow hypanthia (Figs. 5.1;

5.3A-C), that can appear flat due to the plane of section (Figs. 5.3C; 5.4A). Terminal flowers are trimerous, bearing 6 tepals in two whorls, and 9 stamens in three whorls (Figs. 5.2C, 5.5). Some terminal flowers of the main inflorescence axis appear to have more than 6 tepals, but it is unclear whether these represent tips of enclosing bracts or a third perianth whorl. Penultimate flowers are also trimerous in most specimens, but dimerous flowers are also found in this position on the lateral axes in some specimens (Fig. 5.3D). Dimerous flowers, when present, are predominantly found at antepenultimate positions. In these dimerous flowers there are two tepals and two stamens per whorl, but otherwise, floral organization is identical to that of trimerous flowers (Figs. 5.5, 5.6).

All flowers bear three whorls of stamens, and lack an inner fourth whorl of stamens or staminodes. Stamens of the two outer whorls are introrse, and those of the third innermost whorl are extrorse (Figs. 5.2C-D; 5.3A-C). The third whorl stamens bear a pair of globose appendages near the base of each filament (Fig. 5.3E). Anthers exhibit two sporangial cavities in the most mature flowers (Figs. 5.1A; 5.2C; 5.3A, C-D). Several of these anthers also contain clumps of cells in their sporangia, but it is unclear what stage of development is preserved (Fig. 5.3C-D). It is also difficult to confirm if anthers dehisce by valves, because of the presence of predominantly immature stages.

The paucity of mature flowers makes some floral features difficult to determine. Filaments are shorter than the anthers (Fig. 5.3), and more mature flowers have longer filaments. Additionally, inner tepals are smaller than the outer tepals in bud (Fig. 5.2C-D), but look similar in size in mature flowers (Fig. 5.4A). However, it is difficult to assess precise lengths of these floral organs in the most mature flowers due to incomplete preservation (Fig. 5.4A).

The gynoecium is formed from a single carpel in all flowers. The gynoecium is superior and contains a single, apically attached ovule (Fig. 5.4A, B). The style is short in immature flowers, ending in a stigma near the level of the anthers. Stigmas do not appear to be large or distinct, but this may be due to the early developmental stages observed. In more mature flowers, the gynoecium is enlarged, but the style is still placed near the level of the anthers (Fig. 5.4A).

Trichomes occur on various surfaces of the inflorescence organs (Figs. 5.2B, 5.4C). They are about 3 μm in diam, but length is variable. All trichomes are unbranched, uniseriate, and terminate in an acute tip. Each trichome base is a modified epidermal cell (Fig. 5.4C), and occasionally, trichomes appear septate (Fig. 5.4C). Abaxial bract surfaces bear more trichomes than adaxial bract surfaces. Trichomes are more dense on bracts (Figs. 5.1; 5.2A, B), and less abundant on tepals (Figs. 5.2; 5.3A-C; 5.4A). In addition, some trichomes occur on the base of the flower, in the hypanthium, near the gynoecium (Fig. 5.3A, arrows), but not on the surface of the stamens or the gynoecium (Figs. 5.3; 5.4A).

Sclereids are present in the ground tissues of bract mid-ribs, and are arranged in small groups, or sometimes isolated (Figs. 5.2B; 5.4D). Branched and unbranched pits are abundant in sclereid cell walls (Fig. 5.4C, D). Similar sclereid clusters are seen in the parenchymatous pith of inflorescence axes.

Tracheary elements in the inflorescence axis have helical and annular secondary wall thickenings. Scalariform secondary wall thickenings are also present in tracheary elements near bases of the inflorescence axes. Tracheary elements in bract midveins have annular to scalariform secondary wall thickenings. In the basalmost portions of some inflorescence axes, a ring of secondary xylem is present.

Large, spherical cells are present throughout all the organs of the inflorescences (Figs. 5.1; 5.2; 5.3; 5.4). These idioblasts probably contained oil or mucilage. Contents of the idioblasts are typically a yellow to golden color, but can also appear darker, approaching brown to black.

## DISCUSSION

Trimerous flowers with two whorls of tepals, three whorls of stamens, a fourth androecial whorl of staminodes, a superior ovary composed of a single carpel containing one, apical ovule are typical of Lauraceae (Cronquist 1981; Watson and Dallwitz 1992; Judd et al. 2002). In addition, flowers in this family have stamens that dehisce by more-or-less apically hinged valves, and hypanthia that are flat to deeply urceolate (Endress and Hufford 1989; Rohwer 1993). Inflorescences in Lauraceae are panicles with cymose lateral axes, panicles with racemose lateral axes, racemes, botryoids, or pseudo-umbels of one to several flowers (Kostermans 1957; Rohwer 1993; van der Werff 2001; Frumin et al. 2004).

Fossil specimens consist of immature inflorescences and some isolated segments, including flowers. Both trimerous and dimerous flowers are present in the fossil inflorescences (Fig. 5.5), with dimerous flowers found at non-terminal positions (Fig. 5.6). Inflorescences are enclosed in pubescent bracts from the base, and each lateral subunit is also enclosed in bracts. Inflorescences are monotelic, as the main axis is terminated in a single trimerous flower (Troll 1964; Weberling 1983, 1989). Each oppositely-arranged lateral axis also terminates in a flower and has a cymose organization with oppositely arranged penultimate flowers, each enclosed in a bract. This type of paniculate-cymose inflorescence has also been called thyrsopaniculate (Weberling 1985, Rohwer 1993; Rohwer and Rudolph 2005) and corresponds to Lauraceae inflorescence "type 2" sensu van der Werff and Richter (1996; van der Werff 2001).

Floral organization in dimerous flowers is identical to that in trimerous flowers, except that the perianth and androecial whorls have two parts per whorl, versus three parts per whorl in trimerous flowers. All flowers are hermaphroditic and bear floral organs on a shallow hypanthium. Tepals occur in two whorls and are imbricate, enclosing the immature flowers. In more mature flowers, tepals appear more erect. Anthers are bisporangiate and occur in three whorls. In bud, stamen filaments are shorter than the anthers, but in more mature flowers, filaments may be proportionately longer. Anthers are introrse in the outer two whorls, and extrorse in the innermost, third whorl, although the presence of valvate dehiscence cannot be clearly determined in the specimens, due to immaturity. A fourth innermost whorl of stamens or staminodes is absent. Each flower has a superior unicarpellate ovary containing one apical ovule. Styles end near the level of the anthers in both immature and mature flowers. Trichomes appear to be absent from the surfaces of the anthers and carpels, but occur in the hypanthia, adjacent to the ovary, and on the tepals.

In Lauraceae, irregular flowers are known to occur that show deviations from the normal number of tepals, anthers, or carpels (Rohwer et al. 1991; Inoue and Takahashi 1991). In a study of flowers in *Persea americana*, Inoue and Takahashi (1991) found that irregular flowers, where present, have an inconsistent addition or reduction of floral parts that do not conform to a trimerous, dimerous or tetramerous organization. In contrast, the dimerous, fossil flowers have a regular reduction in each whorl, and these flowers always occur at non-terminal positions in the fossil inflorescences. Therefore, it is unlikely that the dimerous flowers in the fossil inflorescences represent teratologies, but rather represent normal, organized flowers, modified as a result of an intra-inflorescence architectural effect due to floral position (Diggle 1997).

*Comparisons to fossil Lauraceae*- Comparisons with extant genera and the known floral fossils of Lauraceae focus on the trimerous flowers of *Similkameena*. The presence of dimery in the fossils is discussed later.

Although there are numerous fossils described as Lauraceae, many fossil species, especially from early paleobotanical work, are probably dubiously identified to species or even genera within this family (Kostermans 1957; Eklund 2000; Kvaček and Eklund 2003). This difficulty is not restricted to fossil remains alone, but is a major problem with field collections, identifications, and classifications in extant Lauraceae (Kostermans 1957, Rohwer 1993, Hyland, 1989, van der Werff 2001), especially if a complete set of reproductive structures (both fruits and flowers) are lacking for a given specimen/collection.

In spite of the numerous descriptions of vegetative lauraceous remains, only about 21 taxa, based on floral remains, are known in the fossil record assignable to Lauraceae or

Laurales (Takahashi et al. 1999, 2001; Eklund 2000). Only a few taxa have inflorescences, or partial inflorescences attached (Drinnan et al. 1990; Eklund and Kvaček 1998; Eklund 2000; Kvaček and Eklund 2003; Frumin et al. 2004). Therefore, comparison of *Similkameena borealis* to the known fossil record is mostly limited to floral characters, with inflorescence characters largely incomparable.

*Fossil taxa: three-dimensionally/anatomically preserved*

Some of the earliest floral remains known for Laurales and Lauraceae occur in the Lower Cretaceous, and are clearly important contributions to the history of the order, but are represented by fragments, making comparisions to *Similkameena* difficult. Crane et al. (1994) described a flower fragment and an isolated lauralean stamen with four pollen sacs, that have apically hinged valves. *Similkameena* bears bisporangiate anthers, and therefore differs from this tetrasporangiate Cretaceous stamen. The flower fragment described by Crane et al. (1994) lacks anthers, and gynoecial characters, but shows stalked staminal appendages and at least one trimerous tepal whorl. These flower fragments may have affinities with other families in Laurales, including Lauraceae, but clearly differ from *Similkameena* in having stalked staminal appendages.

Several other Cretaceous studies describe more complete remains of plants that may be assignable to Lauraceae (Kvaček et Eklund 2003). *Pragocladus lauroides* Kvaček et Eklund (2003) from the Cenomanian of Bohemia was described from partially compressed, charcoalified or lignitized inflorescences with what is probably an indeterminate, primary axis, with helically arranged lateral axes (Kvaček and Eklund 2003). This type of inflorescence is not found in extant Lauraceae (Rohwer 1993; van der

Werff 2001; Kvaček and Eklund 2003) and the authors only assigned this species to Order Laurales. Lateral axes bear helically arranged flowers, that appear sessile (Kvaček and Eklund 2003). Both genera, *Similkameena* and *Pragocladus*, show six tepals in two whorls, and bisporangiate anthers (Kvaček and Eklund 2003), but the paniculate-cymose inflorescences and pedicellate flowers of *Similkameena* distinguish it from the genus *Pragocladus*. Although the flowers known for *Similkameena* are immature, the staminal appendages on the third whorl do not appear stalked as in *Pragocladus* (Kvaček and Eklund 2003).

The extinct genus *Mauldinia* now contains four species from Cretaceous localities in the USA, Europe, and Asia (Drinnan et al. 1990; Eklund and Kvaček 1998; Herendeen et al. 1999; Frumin et al. 2004). All species in the genus have been described from lignitized and/or fusainized specimens. *Mauldinia* species have a central inflorescence axis with helically arranged lateral inflorescence units that are broad, flattened, bilobed, with three to nine flowers (Drinnan et al. 1990; Eklund and Kvaček 1998; Herendeen et al. 1999; Frumin et al. 2004). The bilobed lateral inflorescence axes of *Mauldinia* are distinctive among extinct and extant Lauraceae and are easily distinguished from the lateral units of *Similkameena borealis*. The presence of sessile flowers and a fourth androecial whorl of staminodes in *Mauldinia* also differs from *Similkameena* which has pedicellate flowers and lacks a fourth whorl of staminodes. However, other floral characters of *Mauldinia* match those of *Similkameena*, such as the presence of bisporangiate anthers, glands on the filaments of third whorl stamens, introrse outer stamens, and extrorse third whorl stamens. It is difficult to compare the flowers of

*Mauldinia* to those of *Similkameena*, in regards to trichome distribution, and presence or absence of "perforations"(likely idioblasts) on the surface of organs, due to the different types of preservation. Peel sections, of *Similkameena*, often reduce the ability to observe trichome distribution in detail, and the "perforations" in *Mauldinia* may be idioblasts that would probably appear as perforations in a mature state.

*Neusenia tetrasporangiata* Eklund (2000), and lauraceous "Taxon A" and "Taxon B" were described based on flowers and partial inflorescence fragments from the Neuse River locality (Santonian/Campanian) of North Carolina (Eklund 2000). *Neusenia* is known from a single bisexual, pedicellate, trimerous, flower with six tepals in two whorls, nine tetrasporangiate, valvate stamens in three whorls, a fourth innermost whorl of staminodes, and a unicarpellate gynoecium (Eklund 2000). Outer tepals are slightly shorter than inner tepals, and third whorl stamens have stalked staminal appendages (Eklund 2000). *Similkameena* is similar to *Neusenia* in the overall arrangement of floral organs, but differs in having bisporangiate anthers, and stalked staminal appendages on the third whorl stamens. In addition, *Similkameena* also lacks the fourth innermost whorl of staminodes, seen in *Neusenia.*

Taxon A (Eklund 2000) is represented by inflorescence fragments with three closely-spaced, sessile, trimerous flowers bearing bisporangiate, valvate anthers, and a unicarpellate gynoecium with an apical ovule; the flower clusters are enclosed by two bracts. Specimens of Taxon A were considered to be immature since dissection did not allow the confirmation of all details of floral arrangement, such as the presence of a staminodal whorl or the presence of staminal appendages (Eklund 2000). Tepals, probably six in two whorls, are partially fused at the base and form a shallow floral tube (Eklund 2000). One interpretation of Taxon A is that it possesses a cymose inflorescence subunit with enclosing bracts surrounding the flowers (Eklund 2000), similar to those of *Similkameena*. *Similkameena* has bisporangiate anthers like in Taxon A, but differs from Taxon A in having pedicellate flowers.

Taxon B (Eklund 2000) is represented by fragmentary flowers and one fruit. Flowers of Taxon B have six tepals in two whorls, stamens with paired appendages on filaments, and a superior unicarpellate ovary, but arrangement and number of stamens, as well as sporangial number per anther could not be determined (Eklund 2000). Therefore, comparison to *Similkameena* is difficult, and although the few known characters of Taxon B are similar to *Similkameena*, more material is needed for Taxon B before details of affinities can determined.

*Lauranthus futabensis* Takahashi, Herendeen et Crane (2001) and "hypogynous flower type 2" (Takahashi et al. 1999) are known from the Kamikitaba locality (Lower Coniacian) of northeastern Japan. Flowers are anatomically preserved carbonaceous mesofossils (Takahashi et al. 1999, 2001). Hypogynous flower type 2 is known from fifteen specimens that are pedicellate, trimerous, bearing six tepals in two whorls, and tetrasporangiate anthers. The presence of a staminodal whorl and staminal appendages is not reported, and stamen number is uncertain, but may be six or nine (Takahashi et al. 1999). In addition, flowers have a superior unicarpellate ovary with fruits developed on a shallow cup-like receptacle and persistent perianth parts, typical of Lauraceae (Takahashi et al. 1999). Flowers have six outer introrse stamens and an innermost whorl of latrorse stamens (Takahashi et al. 1999, 2001). These staminate flowers have reduced or missing carpels, and are therefore interpreted as probably unisexual (Takahashi et al. 1999, 2001). *Lauranthus futabensis* is known from a single flower and has characters similar to those of "hypogynous flower type 2" (Takahashi et al. 2001). However, *Lauranthus* is distinguished from "hypogynous flower type 2" in having well-developed "hairs" on the inner surface of the tepals (Takahashi et al. 2001). Both of these flowers from the Kamiktaba locality share the basic lauraceous morphology with *Similkameena* in having trimerous flowers, with six tepals in two whorls, and nine stamens in three whorls. However, the presence of tetrasporangiate anthers and potential unisexuality contrast with the bisexual flowers with bisporangiate anthers seen in *Similkameena*.

*Perseanthus crossmanensis* Herendeen, Crepet et Nixon (1994) from the Turonian of New Jersey is known from a single specimen with six tepals in two whorls, an androecium with nine stamen bases in three whorls, plus an innermost, fourth whorl of three staminodes (Herendeen et al. 1994). The flower also has a single carpel with one ovule, typical of Lauraceae (Herendeen et al. 1994). *Perseanthus* is similar to *Similkameena* in perianth, androecium, and gynoecium organization, but the staminal appendages of the third whorl stamens have stalks, that are absent in *Similkameena*. In addition, *Perseanthus* has an innermost, fourth whorl of staminodes, whereas *Similkameena* lacks a staminodal whorl. Details of the anthers are missing (Herendeen et al. 1994), precluding further comparisons.

Conwentz (1886) described three species, based on lauraceous flowers, from the Baltic amber (Late Eocene-Early Oligocene): *Trianthera eusideroxyloides*, *Cinnamomum* *felixii* and *C. prototypum*. As in *Similkameena*, all three taxa have pedicellate, bisexual flowers with six tepals in two whorls, but each has tetrasporangiate anthers, which distinguish them from *Similkameena*. *Cinnamomum felixii* lacks an innermost whorl of staminodes, and is therefore most similar to *Similkameena* among these taxa. *Trianthera eusideroxyloides* has only three stamens (presumably of the third whorl), that lack staminal appendages, and possesses an innermost, fourth whorl of staminodes (Conwentz, 1886). Whereas, *Similkameena* lacks a staminodal whorl, has nine stamens, and staminal appendages on the third whorl stamens. Futher, *T. eusideroxyloides*, appears to have two extra whorls of tepals (Conwentz, 1886), presumably the modification of the two outer stamen whorls into tepaloid structures as seen in some extant Lauraceae (Kostermans 1957; Rohwer 1993; Table 1). *Cinnamomum prototypum* has tetrasporangiate anthers and an innermost staminodal whorl that are both lacking in *Similkameena*. The assignment of two of these flowers to the genus *Cinnamomum* may be dubious (Eklund 2000) as this floral morphology is found in several extant genera (Table 1) and the lack of staminodes in *C. felixii* is not typical for the genus (Table 1). Characters of the fruits and/or inflorescences would be required to establish their affinity to *Cinnamomum*.

It is interesting to note that Conwentz (1886) illustrated *C. polymorphum* Heer, based on a leaf-type in the amber, but the *C. polymorphum* flowers and inflorescences, that Heer (1856) described attached to this leaf-type, were not found in the amber. Thus, the attachment of the leaf-type to another flower form is then possible in the amber, and the need for detailed studies to connect isolated organs at fossil localities is indicated.

*Fossil taxa: compression/impressions*

*Cinnamomum polymorphum* was described based on compressions from the Early to Late Miocene of Switzerland and Germany (Heer 1856). The specimens include open, isolated flowers, and branches with racemose inflorescences in bud stage, with attached leaves. Flowers have six equally-sized tepals, in two whorls, six stamens and a single carpel. Flowers *Similkameena* have nine stamens, rather than six, and thyrsopaniculate inflorescences, rather than racemes. The number of anther locules, and other anatomical details are not known for *C. polymorphum*.

*Litseopsis rottensis* Weyland and *Lindera rottensis* Weyland were described based on compressions from the Late Oligocene of Germany (Weyland 1938). *Litseopsis* has flowers with six tetrasporangiate valvate anthers, some appearing to have appendages, but few other characters can be discussed due to the small number of specimens and incomplete preservation. Weyland (1938) thought *Litseopsis* to be bisexual, but also indicated that the structure interpreted as the gynoecium could be nonfloral debris. The six tetrasporangiate anthers clearly differ from the nine, bisporangiate anthers of *Similkameena*, and the potenially unisexual nature of *Litseopsis*, (remaining to be determined), would also differ from *Similkameena*. Flowers of *Lindera rottensis* are unisexual, with only male flowers known (Weyland 1938). An inflorescence fragment has been described, with with three pedicellate flowers attached at the same node, forming a loose pseudo-umbel, and flowers have six tepals in two whorls, six bisporangiate anthers with valvate dehiscence, and staminal appendages of uncertain placement in the flower (Weyland 1938). *Lindera rottensis* may be better placed in the genus *Iteadaphne* (Eklund 2000; Table 1), but nevertheless, *Similkameena* contrasts with *Lindera rottensis* in having bisexual flowers, with nine stamens in trimerous flowers, and an inflorescence with a cymose terminal unit.

*Androglandula tennessensis* Taylor (1988) was described from eight compressed flowers from the Middle Eocene of Tennessee. Each pedicellate flower has a subtending bract, six tepals in two whorls, forming a hypanthium, and a single carpel, as seen in flowers of *Similkameena*. Since flowers are isolated, the inflorescence type is unknown (Taylor 1988), making comparisons to the inflorescence of *Similkameena* impossible. The number of stamens per flower is uncertain, but anthers are interpreted as tetrasporangiate (Taylor 1988), unlike the bisporangiate anthers of *Similkameena*. However, stamens do show short filaments, appearing nearly sessile, and some have staminal appendages (Taylor 1988), as seen in *Similkameena*.

Chaney and Mason (1933) assigned fossil remains, from the Pleistocene asphalt deposits in California, to the extant genus *Umbellularia* (Nees) Nutt. *Umbellularia californica* (Hook. & Arn.) Nutt. is the only extant species in the genus (Rohwer 1993). The trimerous, pedicellate, perigynous, unicarpellate fossil flowers have a six-lobed, undifferentiated perianth, stamens in two whorls, the outer whorl with paired staminal appendages, and tetrasporangiate anthers with two lateral valves (Chaney and Mason 1933). Misidentification of these fossil remains is possible since extant *Umbellularia californica* has four androecial whorls, and the third whorl filaments bear staminal appendages (Table 1), contrasting with the fossil described by Chaney and Mason (1933). However, the Pleistocene *Umbellularia* can be distinguished from *Similkameena* by the number of stamen whorls and the number of locules per anther. In addition, staminal appendages occur on third whorl filaments in *Similkameena*, versus the outermost whorl in fossil *Umbellularia*.

*Comparisons to extant Lauraceae-* Intrafamilial groups in Lauraceae have been distinguished by characters of the inflorescence type, presence/absence of persistent involucra below the inflorescence, fruit cupule presence/absence, flower sexuality, number of stamens, anther orientation, and number of sporangia per anther (Meissner 1864; Pax 1891; Kostermans 1957; Hutchinson 1964, Rohwer 1993). More recently, wood and bark anatomical characters have been used with inflorescence characters (van der Werff and Richter 1996; van der Werff 2001; Li et al. 2004). These intrafamilial groups are well-summarized by Raj and van der Werff (1988), van der Werff and Richter (1996) and Eklund (2000). However, the groups based on morphology are not completely consistent with more recent DNA based phylogenetic analyses (Rohwer 2000; Chanderbali et al. 2001; Rohwer and Rudolph 2005). In addition, morphological generic concepts have been commonly questioned in the literature (e.g., Hyland 1989; Li and Christophel 2000). It is clear that further study is needed to address these problems, and to elucidate the boundaries between genera, which will be difficult due to the difficulties in collection and identification of tropical lauraceous taxa (van der Werff 2001). Also, homoplasy in morphological characters is likely (Rohwer 1993; Eklund 2000; Li and Christophel 2000). Therefore, this chapter avoids attempting to use any particular classification, and restricts comparisons of the fossil *Similkameena borealis* with the current generic concepts in extant Lauraceae, using characters of inflorescences and flowers (Table 1). It is probable that generic concepts and groupings in Lauraceae will be modified upon further study, but based on current concepts, *Similkameena* represents a distinct taxon in Lauraceae.

The presence of trimerous and dimerous flowers in the same inflorescences of *Similkameena borealis* distinguish it from all extant genera of Lauraceae (Table 1). Excluding this diagnostic character state, one can further differentiate the extant genera from the fossils, using characters of inflorescences and the trimerous flowers (Table 1).

While most extant genera have bisexual flowers, several genera are described as having unisexual and/or polygamous flowers (e.g. *Rhodostemonodaphne* Rohwer et Kubitzki, *Laurus* L. in Table 1; Kostermans 1957; Hyland 1989; Rohwer 1993). The presence of a persistent involucre below inflorescences co-occurs with most taxa that are unisexual, but also occurs in the bisexual *Umbellularia*. (Table 1; Kostermans 1957; Rohwer 1993). The bracts associated with the fossil inflorescences may have been persistent, but no complete inflorescences are known at a mature stage of development. Therefore, this character is not used to distinguish *Similkameena* from extant genera.

Numerous genera can be distinguished from *Similkameena* because they lack the inflorescence architecture seen in the Princeton Chert fossils (Table 1). This inflorescence type is called thyrsopaniculate (Weberling 1985, 1989; Rohwer 1993). Using the two characters: thyrsopaniculate inflorescence architecture and floral bisexuality, 25 of the 51 genera can be distinguished from the fossils described here (Table 1). All remaining genera have trimerous flowers, with the exception of *Potameia* Thouars., which has exclusively dimerous flowers (Kostermans 1957) and *Chlorocardium* Rohwer, with exclusively tetramerous flowers (Table 1; Rohwer et al. 1991).

Most of the remaining taxa can be distinguished based on characters of the stamens. In *Similkameena*, there are nine fertile stamens in three whorls in the trimerous flowers. Comparing fertile stamen number in the remaining extant trimerous taxa, six genera (*Aspidostemon* Rohwer & Richter, *Brassiodendron* C.K. Allen, *Endiandra* R.Br., *Eusideroxylon* Teijsm. et Binnend, *Licaria* Aubl., and *Williamodendron* Kubitski & Richter, in Table 1; Rohwer 1993) can be distinguished from the fossil in having consistently fewer than nine fertile stamens per trimerous flower. Other genera already excluded above may have more or fewer fertile stamens than the nine seen in the fossils (e.g., *Hexapora* J. D. Hook.; Table 1; Kostermans 1957). Appendages (often glandular), on the stamen filaments of the third whorl, are a common feature of Lauraceous flowers, including the fossils. The presence and position of these appendages are used as diagnostic characters to define genera (Rohwer 1993); e.g., *Urbanodendron* Mez has appendages on all stamens (Rohwer 1993; Table 1). Other already excluded genera may lack these appendages (e.g., *Williamodendron* Kubitzki & Richter (1987); Table 1), or they may be present on several whorls, or all stamens (e.g., *Cinnadenia* Kosterm.; Table 1; Kostermans 1973). The presence of an innermost staminodal whorl in several remaining genera (*Cinnamomum* Scheaff., *Persea* Mill., *Phoebe* Nees., *Apollonias* Nees., *Nothaphoebe* Blume, *Alseodaphne* Nees., *Caryodaphnopsis* Airy-Shaw, *Aiouea* Aubl., *Nectandra* Rolander ex. Rottb., *Pleurothyrium* Nees ex. Lindl. and *Cryptocarya* R. Br; Table 1; Rohwer 1993) distinguishes them from the Princeton Chert specimens, which lack a staminodal whorl. The number of sporangia per anther in *Povedadaphne* Burger and *Hypodaphnis* Stapf. is consistently four (Rohwer 1993), while in *Similkameena*, each anther consistently has two sporangia (Table 1). Some previously differentiated genera above also have tetrasporangiate anthers (e.g., *Sextonia* van der Werff 1997), or one sporangium per anther (e.g., *Endiandra* R. Br., one species; Hyland 1989), further distinguishing them from the Princeton species. Additionally, *Hypodaphnis* is also unique among lauraceous genera in having a completely inferior ovary (Table 1; Kostermans 1957).

The filament length in relation to anther size is sometimes used in generic concepts, as well as, inner, versus outer, tepal length (Kostermans 1957, Rohwer 1993, 1994, van der Werff 2001). Due to the predominance of immature stages of *Similkameena*, it is unclear to what degree tepals remain slightly unequal in size, or to what degree filament length increased upon maturity. Therefore, I did not use these two features as reliable characters for comparison, and they are excluded from Table 1.

Receptacle shape, although a somewhat subjective character, varies from flat to deeply urceolate in the family (Table 1; Kostermans 1957; Mai 1971; Rohwer 1993). The Princeton flowers have a shallow hypanthium, whereas *Dehaasia* Blume has a cup-shaped receptacle, *Systemonodaphne* Mez. a tubular shape, and *Aniba* Aubl. a deeply urceolate to tubular-shaped receptacle (Table 1; Kostermans 1957; Rohwer 1993) . The one remaining genus, *Ocotea* Aubl., the taxonomic "dust bin of Lauraceae" (Rohwer 1993), is a heterogeneous and polyphyletic assemblage of species (Chanderbali et al. 2001) that shares some characters with *Similkameena*. However, all *Ocotea* have strictly trimerous flowers, in contrast to the Princeton Chert plants with dimerous and trimerous flowers. Furthermore, the majority of species in this genus possess tetrasporangiate anthers, often with latrorse dehiscence of some pollen sacs (Rohwer 1993), while *Similkameena* has bisporangiate anthers and introrse outer stamens, with an extrorse innermost stamen whorl (Table 1).

It is perhaps surprising, in such a speciose family as Lauraceae, that the fossil remains are distinct and represent a new taxon with a unique combination of characters. The presence of thyrsopaniculate inflorescences, with both dimerous and trimerous flowers, is not found in any extinct or extant genus of Lauraceae. Even excluding the presence of dimerous flowers, the trimerous flowers and inflorescences of *Similkameena* can be distinguished from all known fossil and extant Lauraceae.

### *Conclusions*

Reconstructing fossil taxa of Lauraceae could greatly improve the resolution of our knowledge of the evolutionary changes in the family. For example, one of the best known fossil Lauraceae, *Mauldinia mirabilis* Drinnan, Crane, Friis et Pedersen has been found to produce the wood-type *Paraphyllanthoxylon marylandense* Herendeen, through a study of the secondary xylem in an inflorescence axis (Herendeen 1991). In addition, other enigmatic remains, such as those of *Prisca reynoldsii* Retallack and Dilcher (1981) should be reinvestigated to understand their suspected relationship to *Mauldinia* (Drinnan et al. 1990, Eklund and Kvaček 1998). Other lauraceous remains at the Princeton Chert, that are associated with the inflorescences of *Similkameena*, will be the subject of chapter 6.

The Princeton Chert specimens allow for an unprecedented opportunity to study whole inflorescence morphology, since numerous axes are preserved in bud. The remains, described here as *Similkameena borealis*, represent the first and only unequivocal occurrence of the modern thyrsopaniculate inflorescence architecture in the fossil record. In addition, this morphotaxon is one of the few based on floral remains in North America (Taylor 1988), and the only taxon known anatomically from the Paleogene of North America. The unique combination of characters present in *Similkameena* highlights the potential importance of fossils for understanding evolutionary change over time. Future work will focus on the co-occurring reproductive and vegetative remains at Princeton to determine if an expanded set of characters can be established, with the goal of producing a whole-plant concept of *Similkameena borealis*. Given past successes with similar efforts for other taxa present in the Princeton Chert (i.e. Lythraceae; Little and Stockey 2003, 2006; Little et al. 2004), and given the sheer volume of material available for study, we remain confident that this goal is indeed attainable.

## LITERATURE CITED

BASINGER, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 59: 2379-2410.

BASINGER, J. F. and G. W. ROTHWELL. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 55: 1984-1990.

BONEHAM, R. F. 1968. *Palynology of three Tertiary coal basins in south central British Columbia.* Ph.D. dissertation. Ann Arbor, MI: University of Michigan.

BOYLE, E.. M. 1980. Vascular anatomy of the flower, seed, and fruit of *Lindera benzoin. Bulletin of the Torrey Botanical Club*. 107:409-417.

CEVALLOS-FERRIZ, S. R. S., R. A. STOCKEY, and K. B. PIGG. 1991. The Princeton chert: evidence for *in situ* aquatic plants. *Review of Palaeobotany and Palynology* 70: 173-185.

CHANDERBALI, A. S., H. VAN DER WERFF, and S. S. RENNER. 2001. Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104-134.

CHANEY, R.W. and MASON, H.L. 1933. A Pleistocene flora from the asphalt deposits at Carpinteria, California. *Publication 415. Washington, DC: Carnegie Institute of Washington*: 45–79.

CONWENTZ, H. 1886. *Die Flora des Bernsteins Vol. 2 Die Angiospermen des Bernsteins.* Danzig: Willhelm Engelmann.

CRANE, P. R., E. M. FRIIS, K. R. PEDERSEN. 1994. Palaeobotanical evidence on the early radiation of magnoliid angiosperms. *Plant Systematics and Evolution Supplement* 8: 51–72.

CRONQUIST, A. 1981. *An integrated system of classification of flowering plants*. New York: Columbia University Press.

DIGGLE, P. K. 1997. Ontogenetic and floral morphology: the effects of architecture and resource limitation. *International Journal of Plant Sciences* 158: S99-S107.

DRINNAN, A. N., P. C. CRANE, E. M. FRIIS, and K. R. PEDERSEN.1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of Eastern North America. *Botanical Gazatte* 151: 370-384.

EKLUND, H. 1999. *Big survivors with small flowers: fossil history and evolution of Laurales and Chloranthaceae*. Ph.D. dissertation. Faculty of Science and Technology, University of Uppsala, Uppsala. 52 pp..

EKLUND, H. 2000. Lauraceous flowers from the Late Cretaceous of North Carolina, U.S.A. *Botanical Journal of the Linnean Society* 132: 397–428.

EKLUND H and J. KVAČEK. 1998. Lauraceous inflorescences and flowers from the Cenomanian of Bohemia (Czech Republic, Central Europe). *International Journal of Plant Sciences* 159: 668–686.

ENDRESS, P. K. and L. D. HUFFORD. 1989. The diversity of stamen structures and dehiscence patterns among Magnoliidae. *Botanical Journal of the Linnean Society* 100: 45–85.

FERGUSON D. K. 1974. On the taxonomy of recent and fossil species of *Laurus*

(Lauraceae). *Botanical Journal of the Linnean Society* 68: 51–72.

FRUMIN, S., H. EKLUND, and E. M. FRIIS. 2004. *Mauldinia hirsuta* sp. nov., a new member of the extinct genus *Mauldinia* (Lauraceae) from the Late Cretaceous (Cenomanian-Turonian) of Kazakhstan. *International Journal of Plant Sciences* 165: 883-895.

GAZIN, C. L. 1953. The Tillodontia: an early Tertiary order of mammals. *Smithsonian Miscellaneous Collections* 121: 1-110.

HEER O. 1856. *Flora Tertiaria Helvetiae, II. Die apetalen Dicotyledonen*. Winterthur: J. Wurster.

HEO, K., H. VAN DER WERFF, and H. TOBE. 1998. Embryology and relationships of Lauraceae (Laurales). *Botanical Journal of the Linnean Society* 126: 295-322.

HERENDEEN, P. S. 1991. Lauraceous wood from the mid-Cretaceous Potomac Group of eastern North America: *Paraphyllanthoxylon marylandense* sp. nov. *Review of Palaeobotany and Palynology* 69: 277-290.

HERENDEEN, P. S., W. L. CREPET, and K. C. NIXON. 1994. Fossil flowers of Lauraceae from the Upper Cretaceous of New Jersey. *Plant Systematics and Evolution* 189: 29–40.

HERENDEEN P. S., S. MAGALLÓN-PUEBLA, R. LUPIA, P. R. CRANE, and J. KOBYLINSKA. 1999. A preliminary conspectus of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, USA. *Annals of the Missouri Botanical Garden* 86: 407–471.

HILLS, L. V. and H. BAADSGAARD. 1967. Potassium-argon dating of some Lower Tertiary strata in British Columbia. *Bulletin of Canadian Petroleum Geology* 15: 138-149.

HUTCHINSON, J. 1964. *The genera of flowering plants* Vol. 1. Clarendon Press, Oxford.

HYLAND, B. P. M. 1989. A revision of Lauraceae in Australia (excluding *Cassytha*) *Australian Systematic Botany* 2: 135-367

INOUE, H., and B. TAKAHASHI. 1991. Scanning electron microscope observation of abnormal flowers and their frequency in avocado trees. *Journal of the Japanese Society for Horticultural Science* 59: 703-710.

JOY, K. W., A. J. WILLIS, and W. S. LACEY. 1956. A rapid cellulose peel technique in palaeobotany. *Annals of Botany N. S.* 20: 635-637.

JUDD W. S, C. S CAMPBELL, E. A KELLOGG, P. F STEVENS, and M. J. DONOGHUE. 2002. Plant systematics: a phylogenetic approach. 2nd ed. Massachusetts: Sinauer Sunderland.

KOSTERMANS, A. J. G. H. 1957. Lauraceae. *Reinwardtia* 4: 193-256.

KOSTERMANS, A. J. G. H. 1973. *Cinnadennia* Kosterm. genus novum Lauracearum. *Adansonia* 13: 223-227.

KUBITZKI, K., and H. G. RICHTER. 1987. *Williamodendron* Kubitzki and Richter, a new genus of neotropical Lauraceae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 109: 49-58.

KVAČEK, J. and H. EKLUND. 2003. A report on newly recovered reproductive structures from the Cenomanian of Bohemia (Central Europe). *International Journal of Plant Sciences* 164: 1021-1039.

LI, J. and D. C. CHRISTOPHEL. 2000. Systematic relationships within the *Listea* complex

(Lauraceae): a cladistic analysis based on morphological and leaf cuticle data. *Australian Systematic Botany* 13: 1-13.

LI, J., D. C. CHRISTOPHEL, J. G. CONRAN, and H-W. LI. 2004. Phylogenetic relationships within the 'core' Laureae (*Litsea* complex, Lauraceae) inferred from sequences of the chloroplast gene *mat*K and nuclear ribosomal DNA ITS regions. *Plant Systematics and Evolution* 246: 19-34.

MACPHAIL, M. K. 1980. Fossil and modern *Beilschmiedia* (Lauraceae) pollen in New Zealand. *New Zealand Journal of Botany* 18: 453-457.

MAI, D. H. 1971. Über fossile Lauraceae und Theaceae in Mitteleuropa. *Feddes Repertorium* 82: 313-341.

MEISSNER, C. F. 1864. Lauraceae. Pp 1-260 in *Prodromous systematis naturalis regni vegetabilis*. Vol. 15 ed. V. A. De Candolle. Paris: V. Masson et Sons.

MULLER J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1–142.

PAX, F. 1891. Lauraceae. Pp 106-126 in *Die natürlichen Pflanzenfamilien* Band 3, Teil 2, eds. A. Engler and K. Prantl Leipzig, Germany: Wilhelm Engelmann.

PIGG K. B. and R. A. STOCKEY. 1996. The significance of the Princeton chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. *Washington Geology* 24: 32-36.

RAJ, B. and H. VAN DER WERFF. 1988. A contribution to the pollen morphology of Neotropical Lauraceae. *Annals of the Missouri Botanical Garden* 75: 130-167.

RENNER, S. S. 1998. Phylogenetic affinities of Monimiaceae based on cpDNA gene and spacer sequences. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 61–77.

RENNER, S. S. 1999. Circumscription and phylogeny of the Laurales: evidence from molecular and morphological data. *American Journal of Botany* 86: 1301–1315.

RETALLACK, G. and D. L. DILCHER. 1981. Early angiosperm reproduction: *Prisca reynoldsii*, gen. et sp. nov. from mid-Cretaceous coastal deposits in Kansas, U.S.A. *Palaeontographica Abteilungen B. Paläophytologie* 179: 103–137.

ROHWER, J. G. 1993. Lauraceae. Pp 366–391 in *The families and genera of vascular plants. Vol. 2. Flowering plants, dicotyledons: Magnoliid, Hamamelid, and Caryophyllid families*, eds. K. Kubitzki, Rohwer JG and V. Bittrich: Berlin: Springer Verlag.

ROHWER, J. G. 1994. A note on the evolution of the stamens in the Laurales with emphasis on the Lauraceae. *Botanica Acta* 107: 103–110.

ROHWER, J. G. 2000. Toward a phylogenetic classification of the Lauraceae: Evidence from *mat*K sequences. *Systematic Botany* 25: 60-71.

ROHWER, J. G. and B. RUDOLPH 2005. Jumping genera: The phylogenetic positions of *Cassytha*, *Hypodaphnis*, and *Neocinnamomum* (Lauraceae) based on different analyses of *trn*K intron sequences. *Annals of the Missouri Botanical Garden* 92: 153-178.

ROHWER, J. G., H. G. RICHTER, and H. VAN DER WERFF. 1991. Two new genera of neotropical Lauraceae, and critical remarks on the generic delimitation. *Annals of the Missouri Botanical Garden* 78: 338-400.

ROUSE, G. E. and S. K. SRIVASTAVA. 1970. Detailed morphology, taxonomy and distribution of *Pistillipollenites macgregori*. *Canadian Journal of Botany* 48: 287-292.

RUSSELL, L. S. 1935. A Middle Eocene mammal from British Columbia. *American Journal of Sciences* 29: 54-55.

SUN, Z., AND R. A. STOCKEY. 1991. Lauraceous inflorescences from the Middle Eocene Princeton Chert (Allenby Formation) of British Columbia, Canada. *American Journal of Botany supplement* 78: Abstract 323.

STOCKEY, R. A. 1983. *Pinus driftwoodensis* sp. nov. from the early Tertiary of British Columbia. *Botanical Gazette* 144: 148-156.

TAKAHASHI, M., P.R. CRANE, and H. ANDO. 1999. Fossil flowers and associated plant fossils from the Kamikitaba locality (Ashizawa Formation, Futaba Group, Lower Conianican, Upper Cretaceous) of Northeast Japan. *Journal of Plant Research* 112: 187-206.

TAKAHASHI, M., P. S. HERENDEEN, and P. R. CRANE. 2001. Lauraceous fossil flower from the Kamikitaba Locality (Lower Coniacian; Upper Cretaceous) in Northeastern Japan. *Journal of Plant Research* 114: 429-434.

TAYLOR, D. W. 1988. Eocene floral evidence of Lauraceae: Corroboration of the North American megafossil record. *American Journal of Botany* 75: 948-957.

TROLL, W. 1964. *Die Infloreszenzen, Typologie und Stellung im Aufbau des Vegetationskörpers* Vol. 1. Stüttgart: G. Fischer.

WATSON, L., and M.. J. DALLWITZ. 1992 onwards. *The families of flowering plants:*

*descriptions, illustrations, identification, and information retrieval*. Version: 23rd October 2005. http://delta-intkey.com.

WEBERLING, F. 1983. Fundamental features of modern inflorescence morphology. *Bothalia* 14: 917-922.

WEBERLING, F. 1985. Zur Inforeszenmorphologie der Lauraceae. *Botanische Jahrbücher für Systematik und Pflanzengeographie* 107: 395-414.

WEBERLING, F. 1989. *Morphology of flowers and inflorescences*. Cambridge, England: Cambridge University Press.

WERFF, H. VAN DER. 1997. *Sextonia*, and new genus of Lauraceae from South America. *Novon* 7: 436-439.

WERFF, H. VAN DER. 2001. An annotated key to the genera of Lauraceae in the Flora Malesiana region. *Blumea* 46: 125-140.

WERFF, H. VAN DER and H. G. RICHTER. 1996. Toward an improved classification of Lauraceae. *Annals of the Missouri Botanical Garden* 83: 409–418.

WEYLAND, H. 1938. Beiträge zur Kenntnis der rheinischen Tertiärflora. III. Zweite Ergänzungen und Berichtigungen zur Flora der Blätterkohle und des Polierschieffers von Rott im Siebengebirge. *Palaeontographica Abteilungen B. Paläophytologie* 83: 123-171.

WILSON, M. V. H. 1977. Middle Eocene freshwater fishes from British Columbia. *Royal Ontario Museum, Life Sciences Contributions* 113: 1-61.

WILSON, M. V. H. 1982. A new species of *Amia* from the Middle Eocene of British Columbia. *Palaeontology* 25: 413-424.

**Fig. 5.1.** *Similkameena borealis* gen. et sp. nov. longitudinal sections of inflorescences. Scale bars = 0.5 mm A. Inflorescence showing main axis, terminal flower, enclosing pubescent bracts, and lateral cymose axes with flowers in various planes of section, holotype, P1332 $B_1$ bot #6. B. Inflorescence showing main axis, abraded terminal flower, bracts, and lateral cymose axes with flowers in various planes of section, paratype, P1312$B_1$ top #13.

Fig. 5.1

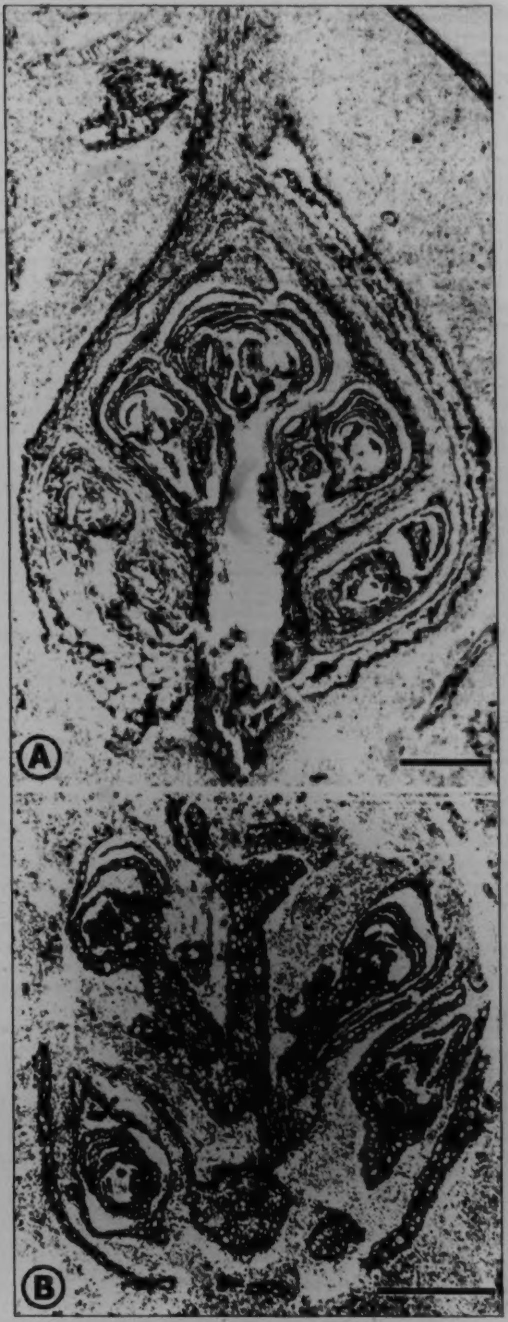

**Fig. 5.2.** *Similkameena borealis* gen. et sp. nov., inflorescences. Scale bars A, B = 0.5 mm. Transverse sections through flowers Scale bars C, D = 0.1 mm. A. Longitudinal inflorescence with enclosing pubescent bracts. Note: two oppositely arranged penultimate flowers in oblique section at lower, center, holotype, P1332 $B_1$ bot #28. B. Close up in same peel series as A. showing pubescent bracts, lateral axis, and oppositely arranged penultimate flowers (arrows). Trimerous terminal flower in oblique section at upper right, and terminal flower pedicel (at *), holotype, P1332 $B_1$ bot #31. C. Transverse section of trimerous flower, with six tepals (T) in two whorls, and nine stamens (S), paratype, P1060 $D_2$ bot#16. D. Transverse section through dimerous flower, with four tepals (T) in two whorls, six stamens (S) in three whorls, and gynoecium (G), paratype, P1349 C bot #9.

Fig. 5.2

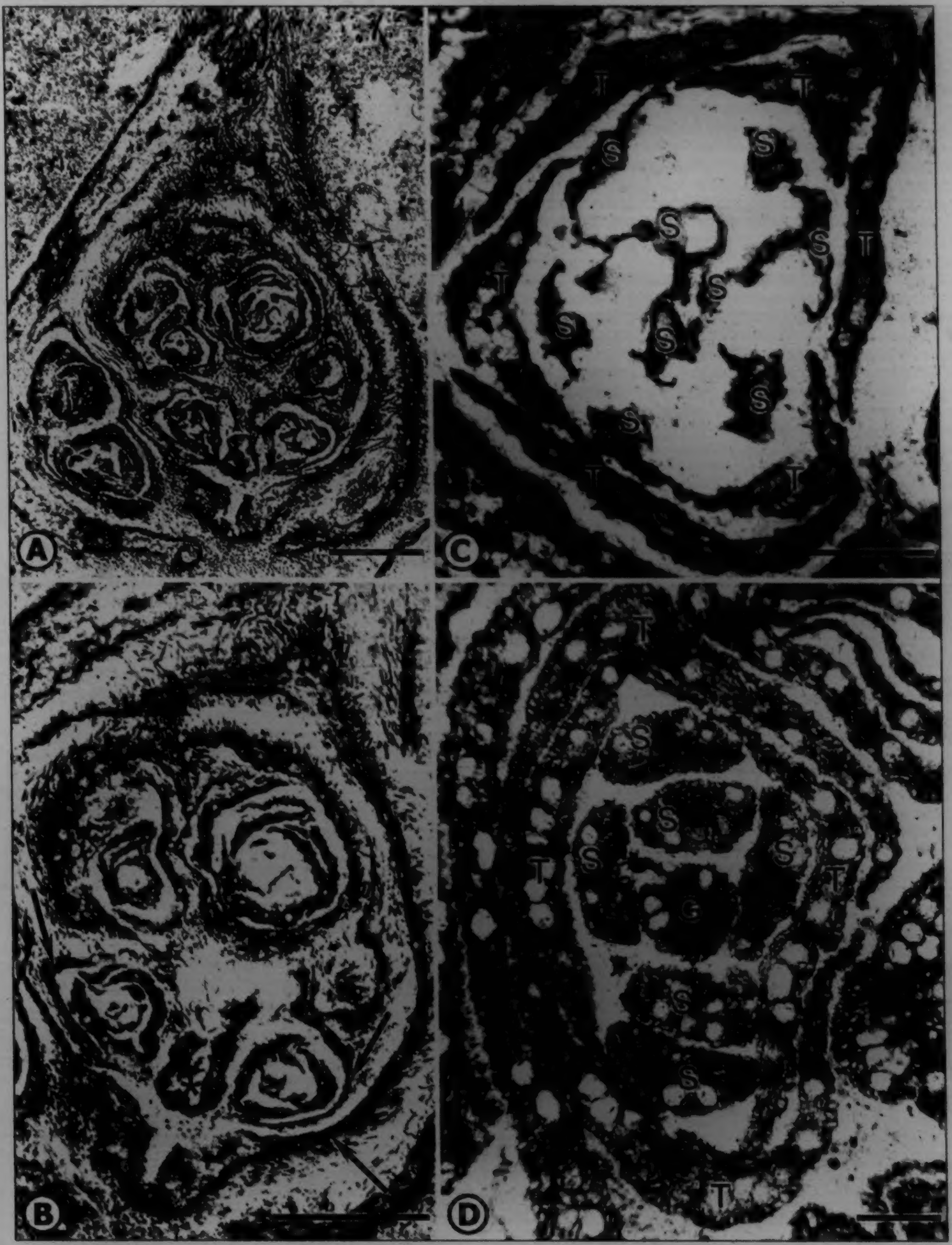

**Fig. 5.3.** *Similkameena borealis* gen. et sp. nov., longitudinal sections through flowers. Scale bars A, B, C = 0.25 mm; Scale bars D, E = 0.03 mm A. Terminal, trimerous flower showing tips of two enclosing bracts (B) six tepals (T), four stamens (S), and gynoecium (G); stamen at right showing one of two sporangial cavities; arrows at trichomes, holotype, P1332 $B_1$ bot #5. B. Terminal, trimerous flower showing tepals, four stamens, and gynoecium (G), paratype, P1237 $D_2$ bot #24. C. Trimerous flower showing tepals, three stamens, and two staminal appendages at base of stamen filaments (arrows); note contents in sporangial cavity in anther at left, holotype, P1332 $B_1$ bot #15. D. Closer view of C showing sporangial contents at left and idioblasts at right, holotype, P1332 $B_1$ bot #15. E. Section through flower showing gynoecium at bottom left, and inner whorl stamen with globose appendage near base of filament (arrow), paratype, P1237 $D_2$ bot #5.

Fig. 5.3

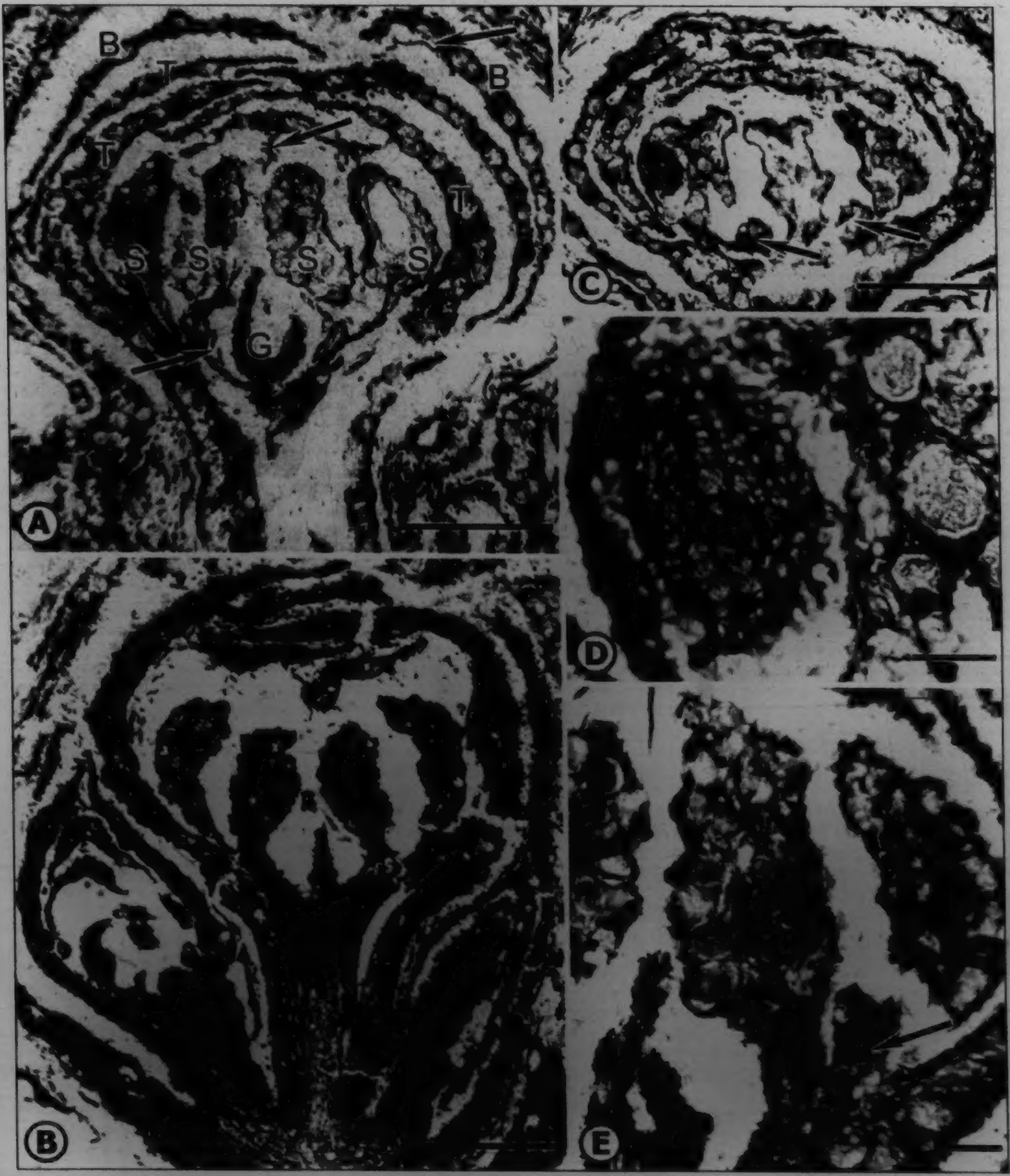

**Fig. 5.4.** *Similkameena borealis* gen. et sp. nov., floral structure and details of inflorescence tissues. Scale bar A = 0.25 mm; Scale bars B, C, D, E = 0.05 mm. A. Longitudinal section pedicellate flower bearing slightly enlarged carpel with single ovule (O), paratype, P1213 $D_2$ bot #0. B. Transverse section of gynoecium, with single ovule (at center) and idioblasts in carpel wall, paratype, P1349 C bot #25. C. Edge of pubescent bract with an isolated sclereid at top; trichomes are occasionally septate (arrows), bases are single epidermal cells (arrowheads), holotype, P1332 $C_2$ bot #11. D. Sclerieds of inflorescence axis, with thick walls and intercellular pitting, paratype, P1288 $C_2$ bot #11. E. Idioblasts with and without contents that occur in all organs, paratype, P1089 $C_2$ side #19.

Fig. 5.4

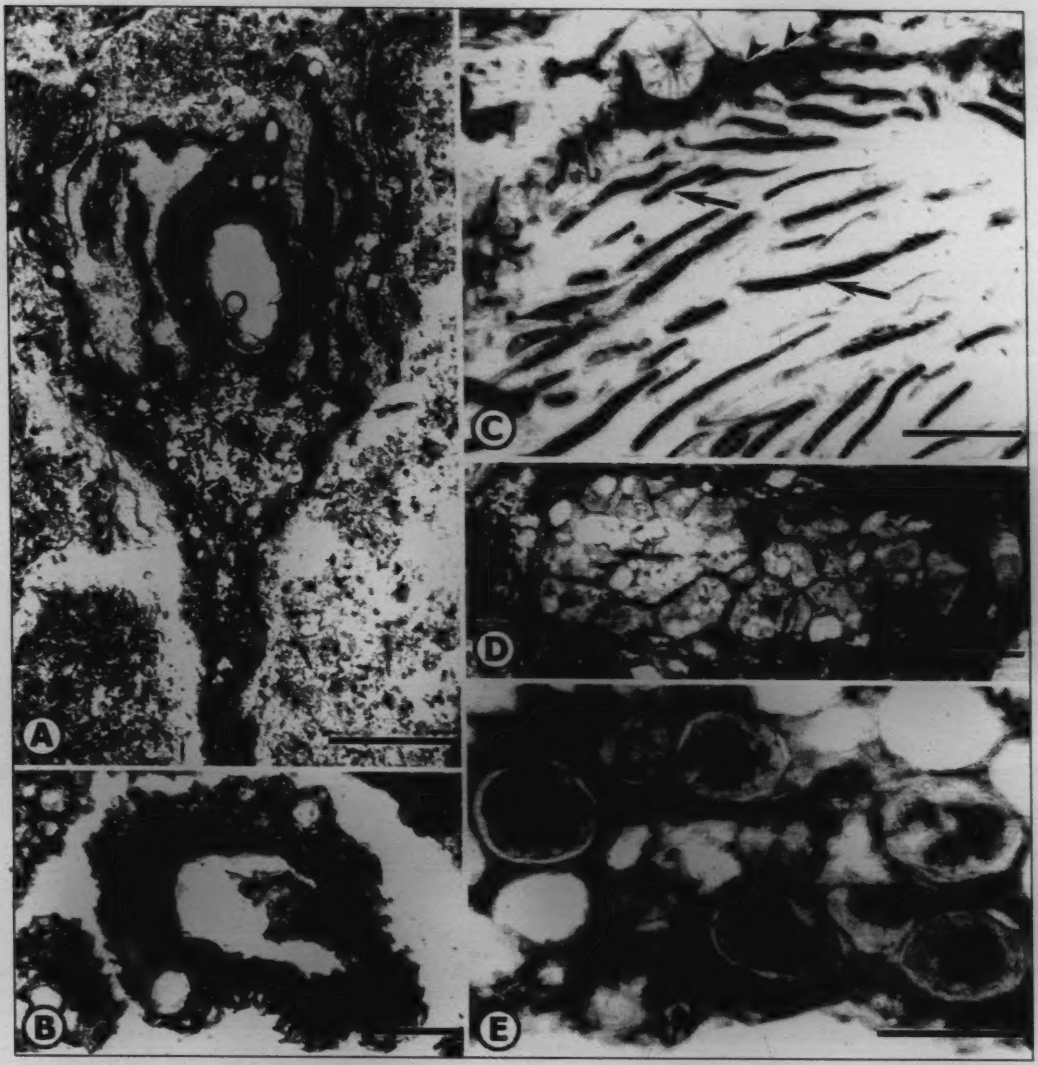

**Fig. 5.5.** *Similkameena borealis* gen. et sp. nov., floral; diagrams. A. Floral diagram of the trimerous flowers. B. Floral diagram of dimerous flowers that occur at non-terminal positions.

Fig. 5.5

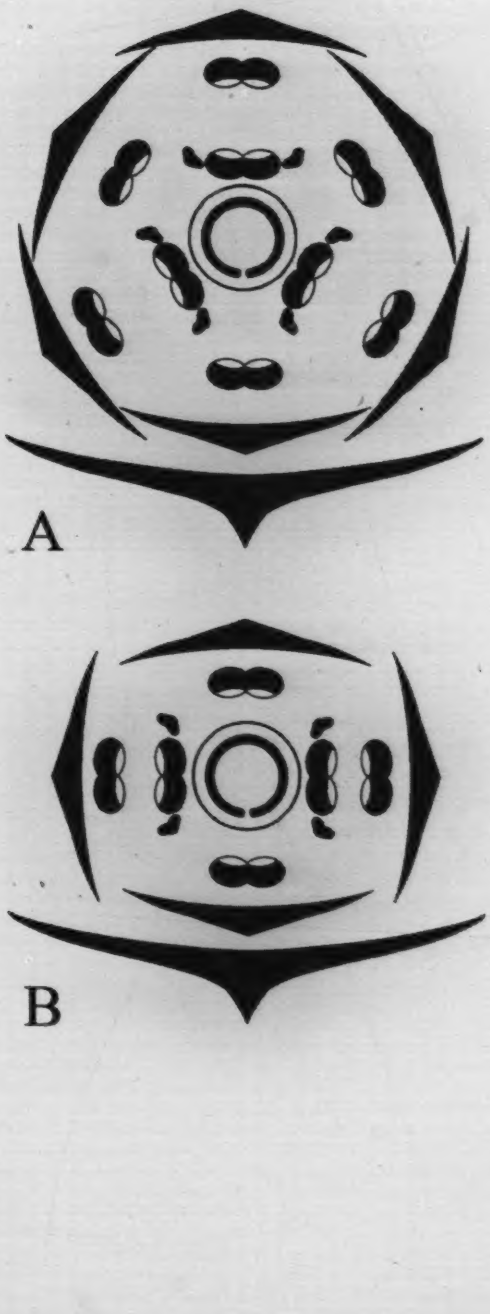

**Fig. 5.6.** *Similkameena borealis* gen. et sp. nov., diagram of inflorescence lateral subunit. Trimerous flowers occur at terminal and penultimate positions. Dimerous flowers can occur at penultimate or other non-terminal positions.

Fig. 5.6

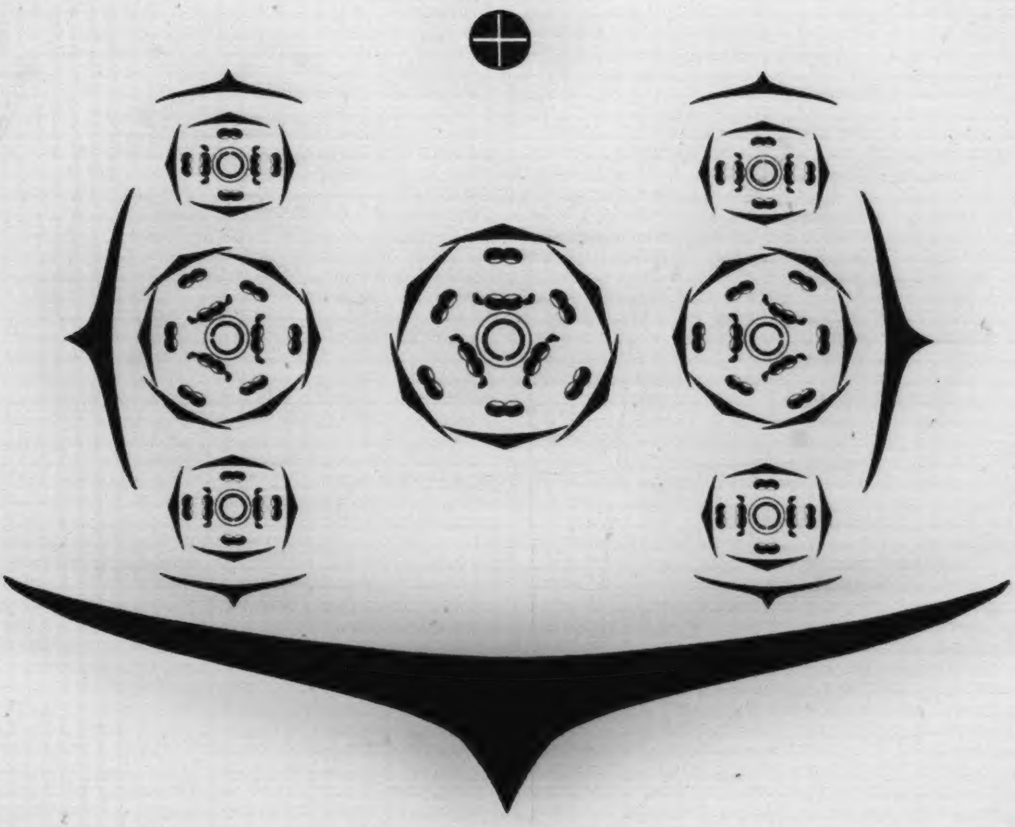

**Table 5.1**. Inflorescence and flower characters of extant genera of Lauraceae.

Legend:

* Numbers listed in this column refer to whorl numbers, with outer whorl as "1"

*Systemonodaphne* = (*Kubitzkia* van der Werff); *Cryptocarya* (= *Ravensara* Sonn.);

*Licaria* (= *Gamanthera* van der Werff )

TP = Thyrsopaniculate; Bo = Botryoid; diBo = Dibotryoid;

P = noncymose panicle (often racemose); Ra = raceme;

Fa = sessile or pedunculate fasicles; Sp = spicate; Um = Pseudo-umbel;

sUm = Stalked Pseudo-umbel; Ca = capitellate; Si= single flower;

sSi= stalked single flower; ff= few flowered (#);

fc= flowers clustered; ss= sessile

int = introrse; lat = latrorse; ext = extrorse; apic = apical

Data from Rohwer (1993), Kostermans (1957), van der Werff, (1997).

Table 5.1. Inflorescence and flower characters of the extant genera of Lauraceae.

| | INFLORESCENCE | | FLOWER | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Genera | architecture | Bracts persist | Bi-sexual | Mery | # fertile stamens | stamen whorl with glands | # sporangia per anther | innermost staminodal whorl | flower receptacle | anther orientation * |
| ***Similkameena borealis*** gen. et sp. nov. | Tp | ? | + | 3 and 2 | 9 (6 in (dimerous flowers) | 3 | 2 | abs | shallow | 1 int;<br>2 int;<br>3 ext |
| ***Actinodaphne*** Nees | P, or Um [dble racemes] | + | - | 3 | (±) 9 | 3 | 4 | +;<br>abs in male | male flat;<br>female flat to deep-cup | 1 int (int + lat);<br>2 int (int + lat);<br>3 ext (int + lat);<br>(extra whorls int + lat) |
| ***Alouea*** Aubl. | Tp | - | + (-) | 3 | 9 (6, or 3) | 3 | 2 | + | cup | 1 int;<br>2 int (stmd);<br>3 ext (stmd) |
| ***Alseodaphne*** Nees | Tp (Bo) | - | + | 3 | 9 | 3 | 4 | + | flat | 1 int;<br>2 int;<br>3 ± ext, or ext+lat |
| ***Anaueria*** Kosterm. | Bo | - | + | 3 | 6 | abs | 2 | + | shallow | 1 lat to int;<br>2 lat to int;<br>3 n/a (stmd) |
| ***Aniba*** Aubl. | Tp (Bo) | - | + | 3 | 9, or 6 | 3 | 2 | + minute to abs | deeply urceolate to tubular | 1 apic to int;<br>2 apic to int;<br>3 ext (to lat) (stmd) |
| ***Apollonias*** Nees | Tp | - | + | 3 | 9 | 3 | 2, | + | flat | 1 int;<br>2 int;<br>3 ± ext |
| ***Aspidostemon*** Rohwer & Richter | Tp | - | + | 3 | 6 (3) | 3, ± enlarged, or confluent | 2 | + | deeply urceolate | 1 int to apic;<br>2 int to apic (stmd);<br>3 n/a (stmd) |
| ***Beilschmiedia*** Nees | P | - | + | 3 | 9, or 6 | 3 | 2 (4: 1sp.) | + | flat to shallow | 1 int;<br>2 int;<br>3 ext to almost int (stmd) |
| ***Brassiodendron*** C. K. Allen | Bo, or Tp | - | + | 3, or IR | 6 (5, or 4) | all | 2 (1: by partial fusion) | abs | cup | lat, in both whorls<br>(whorls present unclear) |
| ***Caryodaphnopsis*** Airy-Shaw | Tp (Bo) | - | + | 3 | 9 | 3 | 4, (2, 1sp.) | + | flat | 1 ± int;<br>2 ± int;<br>3 ± ext, or ext+lat |
| ***Cassytha*** L. | Sp, or Ra (P, Ca) | - | + | 3 | 9 (6) | 3 (outgrowths) | 2 | + | shallow,<br>deeply urceolate at anthesis | 1 int;<br>2 int (stmd);<br>3 ext (stmd) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Chlorocardium*<br>Rohwer | Bo, or Tp | - | + | 4, or IR:<br>4-10 tepals | 12-20 | all stamens | 4 | usually abs | deep-cup | 1 lat, + ext-lat;<br>2 lat, + ext-lat;<br>3 lat, + ext-lat;<br>(extra whorls lat, + ext-lat) |
| *Cinnadenia*<br>Kosterm. | P,(Um) | - | - | 3 or 2 | 9-32<br>males | several inner<br>or all | 4 | +;<br>abs in male | male flat;<br>female shallow | 1 int;<br>2 int;<br>3 int<br>(extra whorls int) |
| *Cinnamomum*<br>Schaeff | Tp (Bo) | - | + (-) | 3 | 9 (6) | 3 | 4 (2) | + | shallow | 1 int;<br>2 int;<br>3 ± ext (stmd) |
| *Cryptocarya*<br>R. Br. | P (? Tp) | - | + | 3 | 9 | 3 | 2 | + | deeply urceolate | 1 int;<br>2 int;<br>3 ext |
| *Dahlgrenodendron*<br>van der Merwe &<br>van Wyk | ff (3), cymules | - | + | 3 | 9 | 3 | 2 | + | deeply urceolate | 1 int,<br>2 int<br>3 ext |
| *Dehaasia*<br>Blume | Tp | - | + | 3 | 9 (6) | 3 | 2 | + to abs | ± cup | 1 int;<br>2 int;<br>3 ± ext to lat (stmd) |
| *Dicypellium*<br>Nees & Mart. | Bo | - | + | 3 | 6 | 3 | 4 | abs (+) | deep-cup | 1 as tepals;<br>2 int;<br>3 apic to lat |
| *Dodecadenia*<br>Nees | Si | + | - | 3, or IR:<br>+ tepal # | 12-18 | several inner | 4 | +;<br>abs in male | shallow | 1 int + lat;<br>2 int + lat;<br>3 int + lat;<br>(extra whorls int + lat) |
| *Endiandra*<br>R. Br. | Tp (or Bo) | - | + | 3 (2: 1sp.) | 3 (2, or 6) | 3 (abs) | 2 (1: fusion, 1sp.) | + to abs | flat to shallow | 1 n/a (smd);<br>2 n/a (stmd);<br>3 ± ext, or apic |
| *Endlicheria*<br>Nees | Tp | - | - | 3 | 9 | 3 | 2, (4: whorl 3) | abs | shallow to<br>deeply urceolate | 1 int to lat;<br>2 int to lat;<br>3 ± ext |
| *Eusideroxylon*<br>Teijsm. & Binnend. | Tp | - | + | 3 | 3 | 3 | 4 | + | semi-inferior | 1 small tepaloid;<br>2 small tepaloid;<br>3 lat + int |
| *Hexapora*<br>J. D. Hook. | Bo (? P) | - | + | 3 | 6 | abs | 2 | + | flat | 1 ext;<br>2 ext;<br>3 n/a (stmd) |
| *Hypodaphnis*<br>Stapf | Tp | - | + | 3 | 9 | 3 | 4 | abs | inferior | 1 int;<br>2 int;<br>3 ± ext |
| *Iteadaphne*<br>Blume | short Ra<br>(?Um in series) | + | - | 3, or IR:<br>- tepal # | 6-9<br>males | 3 | 2 | +;<br>+, or abs in male | male flat;<br>female shallow | 1 int;<br>2 int;<br>3 lat, or stmd |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Laurus***<br>L. | ff (5-10) sUm | + | - | **2**, or IR in androecium | 8-9-30 males | several inner | **2** | +;<br>**abs** in male | male flat;<br>female **shallow** | **1 int**;<br>**2 int**;<br>3 int<br>(extra whorls int) |
| ***Licaria***<br>Aubl. | Tp<br>(Bo, Ca, or Si) | - | + | 3 | 3 | 3 (abs) | 2 | +, or **abs** | deeply urceolate | 1 n/a;<br>2 n/a;<br>**3** apic (int to **ext**) |
| ***Lindera***<br>Thunb. | ff (3-15) Um,<br>(in Ra or ss) | + | - | **3**, or IR:<br>0-6 tepals | 9-15 | several inner | **2** | +;<br>**abs** in male | male flat;<br>female **shallow** | **1 int**, or lat;<br>**2 int**, or lat;<br>3 int, or lat;<br>(extra whorls int, or lat) |
| ***Litsea***<br>Lam. | Um,<br>in Ra (ss) | + | - | 3, or IR:<br>0-9 tepals | (5-) **9** (-20)<br>males | **3**, or several<br>inner if +9<br>stamen # | 4 | usually **abs** | male flat;<br>female flat to<br>deep-cup | **1 int** (int + lat);<br>**2 int** (int + lat);<br>**3 ext** (int + lat);<br>(extra whorls ext (int + lat)) |
| ***Mezilaurus***<br>Kuntze ex Taubert | (di)Bo | - | + | 3 | 3 | abs (+: 1sp.) | **2** | +, or **abs** | deeply urceolate | 1 n/a (stmd);<br>2 n/a (stmd);<br>**3** lat, or **ext**, or apic |
| ***Nectandra***<br>Rolander ex Rottb. | **Tp** | - | + | 3 | **9** | 3 | 4 | + | **shallow** to<br>deeply urceolate | **1 int**, or int+lat;<br>**2 int**, or int+lat;<br>**3 ext**, or ext+lat |
| ***Neocinnamomum***<br>Liou Ho | Fa | - | + | 3 | **9** | 3 | 4 | + | flat to deep-cup | 1 int+lat;<br>2 int+lat;<br>3 int+lat, or ext+lat |
| ***Neolitsea***<br>Merr. | ff (3-6) Um,<br>(in Ra, or ss) | + | - | **2** (± IR) | (4-) **6** (-8)<br>males | 3 & 4 | 4 | +;<br>**abs** in male | male flat;<br>female **shallow** | **1 int**;<br>**2 int**;<br>3 int |
| ***Nothaphoebe***<br>Blume | **Tp** | - | + | 3 | **9** | 3 | 4 | + | flat | **1 int**;<br>**2 int**;<br>**3 ± ext** |
| ***Ocotea***<br>Aubl. | Tp, P, Bo | - | +, or - | 3 | 9 | 3 | 4<br>(**2**: some C.A. spp.) | + to **abs** | flat to<br>deeply tubular | **1 int**, or int+lat;<br>**2 int**, or int+lat;<br>3 ext+lat, or variable |
| ***Paraia***<br>Rohwer, Richter &<br>van der Werff | diBo fc | - | + | 3 | **9** | 3 | 4, or **2**: outer whorls | + | deeply tubular | 1 subapic to **int**;<br>2 subapic to **int**;<br>3 subapic to lat |
| ***Parasassafras***<br>Long | Um | + | - | 3 | 9 | 3 | 4<br>(2: "Sinosassafras") | **abs** | flat | **1 int**;<br>**2 int**;<br>3 int |
| ***Persea***<br>Mill. | **Tp** | - | + | 3 | 9, or 6 | 3 | 4<br>(2 in whorl 3, or all 2) | + | flat | **1 ± int**;<br>**2 ± int**;<br>**3 ext** to ± lat (stmd) |
| ***Phoebe***<br>Nees | **Tp** | - | + | 3 | **9** (6) | 3 | 4 | + | flat | **1 int**;<br>**2 int**;<br>**3 ± ext** (stmd) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Phyllostemonodaphne***<br>Kosterm. | ff Bo | - | + | 3 | 6 | all | 2 | **abs** (+, minute) | **shallow** | 1 as tepals;<br>2 **int**;<br>3 lat |
| ***Pleurothyrium***<br>Nees ex Lindl. | Tp | - | + | 3 | 9 | 3, enlarged,<br>or confluent | 4 | + | urceolate | 1 lat to int + lat to ext;<br>2 lat to int + lat to ext;<br>3 lat to int + lat to ext |
| ***Potameia***<br>Thouars | Tp | - | + | 2 | 4 | 3, or abs | 2 (1: in "syndiclis") | +, **abs**: spp.<br>in Madagascar | **shallow** | 1 int to apic;<br>2 int to apic;<br>3 n/a (stmd) |
| ***Potoxylon***<br>Kosterm. | Ra, or Bo | - | + | 3 | 9 | 3 | 4 | + | semi-inferior | 1 **int**;<br>2 **int**;<br>3 **ext** |
| ***Povedadaphne***<br>Burger | Tp | - | + | 3 | 9 | 3 | 4 | **abs** | cup | 1 apic;<br>2 apic;<br>3 apic |
| ***Rhodostemonodaphne***<br>Rohwer & Kubitzki | Tp | - | - | 3 | 9 | 3, (1) | 4 | **abs** | narrow tubular | 1 **int**;<br>2 **int**;<br>3 ± **ext** |
| ***Sassafras***<br>Presl | Bo (Um) | + | - | 3 | 9 | 3 | 2, or 4 | + to **abs** | flat | 1 **int**;<br>2 **int**;<br>3 int |
| ***Sextonia***<br>van der Werff | Ra, or P | - | + | 3 | 9 | 2 & 3 | 4 | + | deep-cup | 1 **int**;<br>2 **int**;<br>3 **ext** |
| ***Systemonodaphne***<br>Mez | Tp-Bo | - | + | 3 | 9 | 3 | 2, or 4 | **abs** | tubular, short | 1 **int**;<br>2 **int**;<br>3 **ext** |
| ***Umbellularia***<br>(Nees) Nutt. | ff(5-10) sUm | + | + | 3 | 9 | 3 | 4 | + | flat | 1 **int**;<br>2 **int**;<br>3 **ext**, lat to int |
| ***Urbanodendron***<br>Mez | Tp, Bo | - | + | 3 | 9 | all | 2, or 4 | **abs** (+) | urceolate | 1 **int** to lat;<br>2 **int** to lat;<br>3 lat (to **ext**) |
| ***Williamodendron***<br>Kubitzki & Richter | Tp, or diBo | - | + | 3 | 3 | abs | 4 | + | deeply urceolate | 1 n/a (stmd);<br>2 n/a (stmd);<br>3 apic |

# CHAPTER 6

## Fruit development and anatomy of *Similkameena borealis* (Lauraceae)

### INTRODUCTION

Lauraceae, a large pantropical family mainly composed of large trees or shrubs, consists of approximately 53 genera and 2500-3000 species, with much of the known diversity described from the Neotropics (Meissner 1864; Pax 1891; Kostermans 1957; Hutchinson 1964, Rohwer 1993, 1999). Molecular phylogenetic studies clearly show the monophyly of the family (Renner, 1998, 1999), and while intergeneric relationships in Lauraceae are becoming established (Rohwer, 2000; Chanderbali et al., 2001; Rohwer and Rudolph, 2005), generic circumscriptions are plagued by polyphyly (Chanderbali et al., 2001; Li et al., 2004), impeding progress. The family is distinguished by trimerous flowers, bi- or tetrasporangiate anthers with apical valvate dehiscence, and a unicarpellate gynoecium containing a single anatropous ovule (Cronquist, 1981; Heo et al., 1998). Fruits of the family are typically dark colored fleshy berries (Roth, 1977), usually borne on enlarged receptacles that can form enclosing or cupulate structures (Kostermans, 1957; Hyland, 1989; Rohwer, 1993). Oil or mucilage idioblasts occur throughout the plant tissues, including the wood (Baas and Gregory, 1985). Anatomy and development are well known in *Persea americana* Mill., the avocado (Roth, 1977), but detailed studies of fruits in the family are few in comparison to the number of species in the family (Corner, 1976; Roth, 1977). Thus, anatomically preserved fossils of Lauraceae, give us a good opportunity to advance our understanding of fruit development and anatomy in the family.

Lauraceae have been historically grouped with Magnoliales, Trimeniaceae, Amborellaceae (Cronquist, 1981; Takhtajan, 1997) and a suite of families now placed in the order Laurales (Thorne, 2000; APG II 2003). Molecular studies consistently place Lauraceae in Order Laurales, with Calycanthaceae, Siparunaceae, Gomortegaceae, Atherospermataceae, Monimiaceae, and Hernandiaceae (Renner, 1998, 1999). However, the sister group relationships between Lauraceae, Monimiaceae, and Hernandiaceae are still considered unresolved (Renner and Chanderbali, 2000). Recent molecular dating of the family has placed its origin in the Early Cretaceous (Renner, 2004 ).

The diverse fossil record of Lauraceae begins in the middle part of the Cretaceous and includes flowers, fruits, leaves, and wood (Drinnan et al., 1990; Herendeen, 1991; Kvaček, 1992; Herendeen et al., 1999; Crane et al., 1994; Eklund and Kvaček, 1998; Mickle, 1996; Frumin et al., 2004). Fossil vegetative remains of Lauraceae are also common in the Paleogene (Weyland, 1938; Krausel, 1938; Dilcher, 1963; Kovach and Dilcher, 1984; Mai and Walther, 1985; Wheeler et al., 1977; Wheeler and Manchester, 2002), and reproductive structures including flowers, fruits, and cupules also occur in the Paleogene to the Quaternary (Heer, 1856; Conwentz, 1886; Berry, 1916; Chaney and Mason, 1933; Reid and Chandler, 1933; Weyland, 1938; Scott, 1954; Kirchheimer, 1957; Chandler, 1964; Mai and Walther, 1985; Taylor, 1988). Pollen is rarely known in the fossil record (Muller, 1981), because the thin to absent exine in Lauraceae has low preservation potential (MacPhail, 1980; Herendeen et al., 1994). The identification of fossil Lauraceae is often difficult (Rohwer, 1993), resulting in the use of broadly circumscribed morphotaxa at the family level, such as *Laurophyllum* Göppert for leaf compressions (Frumin et al., 2004).

Fruits and cupulate structures commonly occur throughout the fossil record (Chandler 1964; Mai 1971, 1999, 2001; Manchester, 1994; Pingen et al., 1994; Eklund, 2000; Frumin et al. 2004), but few are known anatomically, with some exceptions (Drinnan et al. 1990; Eklund and Kvaček. 1998; Frumin et al. 2004). Numerous lauraceous fruits in the Tertiary are assigned to extant genera (Chandler, 1964; Mai, 1971), but several of these assignments are also questioned (Kostermans, 1957; Chandler, 1978; Rohwer, 1993; Pingen et al., 1994). Further systematic anatomical surveys are required in the family to test the accuracy of the generic identifications (Chandler, 1978; Pingen et al., 1994).

This study describes lauraceous fruits first identified by Penner (1996) from the Middle Eocene Princeton Chert. Numerous specimens are known from different developmental stages, and this developmental series reveals a sequence from late flowers of *Similkameena borealis* Little et Stockey, based on inflorescences and flowers, to the latest stages of fruit maturity. This work represents the only known investigation of the development of fossil fruits of Lauraceae, and expands the species concept of *Similkameena borealis*.

## MATERIALS AND METHODS

The Princeton Chert locality has also been called locality "I" (Boneham 1968) and is part of the Princeton Group, Allenby Formation. The chert is found on the east bank of the Similkameen River, ca. 8.4 km southwest of the town of Princeton, British Columbia

(UTM 10U FK 786725; 49°22'33" N, 120°32'18" W). At least forty-nine interbedded layers of chert and coal occur, with occasional ash beds (Stockey, 1983; Cevallos-Ferriz et al., 1991). Several of the chert layers split and anastomose, so that seventy separate chert layers are observed in some places along the 10 m high and 30 m long exposure (pers. observ. 2003). The locality is dated as Middle Eocene; based on data from pollen (Rouse and Srivastava, 1970), fossil mammals (Russell, 1935; Gazin, 1953), fish (Wilson, 1977, 1982), and potassium-argon dating (Hills and Baadsgaard 1967). A new date of 48.7 Ma was recently obtained for ash layer #22 (H. Baadsgaard, personal communication, 1999).

Chert blocks, containing permineralized plants, are collected in bulk, slabbed on an oil-cooled rock saw, and prepared using the cellulose-acetate peel technique (Joy et al., 1956) modified for hydrofluoric acid (Basinger and Rothwell, 1977; Basinger, 1981). All fossil specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Approximately 50 fruits at various stages of maturity were examined. Sections of consecutive peels were mounted with Eukitt rapid mounting medium (O. Kindler, GmbH, Freiburg, Germany) for light microscope examination. Images were taken with a Microlumina (Leaf Systems, Inc.) digital scanning camera and a Phase One digital scanning camera (Phase One A/S, Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe Photoshop. Characters were analyzed, in part, using the Delta Key program (Watson and Dallwitz, 1992).

## SYSTEMATICS

Order: Laurales

Family: Lauraceae Juss.

Genus: *Similkameena* Little et Stockey.

***Amplified diagnosis***: Inflorescences thyrsopaniculate, lateral axes opposite, determinate/cymose. Lateral axes, and penultimate units of lateral axes enclosed by pubescent bracts. Flowers bisexual, actinomorphic. Terminal and penultimate flowers trimerous, with nine bilocular stamens in three whorls, staminodes absent. Basalmost flowers of lateral axes, dimerous with six bilocular stamens in three whorls, staminodes absent. Glandular appendages present near base of stamens in third whorl. Gynoecium unicarpellate, uniloculate, style short; ovule one, apical, anatropous. Trichomes, uniseriate, unbranched. Pith of inflorescence axis with sclereid clusters. Idioblasts present in all organs. Fruits globose, cupules shallow, sclerotic, tepal remnants lacking. Epicarp of radially elongate epidermal cells; outer mesocarp fleshy with numerous idioblasts; inner mesocarp contains sclereid clusters, often with a central idioblast, cells of clusters radiately arranged; vascular strands and cells with dark contents beneath sclereid layer. Endocarp a single palisade layer, cells radially elongate, thick-walled, transverse outline stellate. Mature seed integument thin, vascular strands present throughout, innermost cell layer radially elongate. Embryo large with scattered idioblasts, endosperm lacking.

Species: *Similkameena borealis* Little et Stockey

***Amplified diagnosis***: Inflorescences at least 4.5 mm long and 2.5 mm in diam, bearing at least 15-25 pedicellate flowers. Perianth of six tepals in two whorls in terminal and penultimate flowers of lateral axes; perianth of 4 tepals in two whorls in basalmost flowers of lateral axes. Stamens of outer two whorls introrse, innermost whorl extrorse; immature stamens with short filaments. Tepals sub-equal in immature flowers, inner tepals slightly smaller than outer. Receptacles wide, hypanthium shallow. Trichomes, abundant on bracts, few on tepals, absent from stamens, few around base of gynoecium. Sclereid clusters in pith of inflorescence axes; isolated sclereids present in bract midribs and mesophyll. Idioblasts, up to 70 µm in diam, present in all organs. Fruits 5-8 mm in diam, fruit wall lacking trichomes; cupules sclerotic, extend over lower 10-20% of fruit. Epicarp/epidermal cells 20-40 µm thick. Outer mesocarp fleshy, 16-35 cells thick (0.3-0.5 mm), containing idioblasts 30-60 µm in diam. Sclereid clusters of inner mesocarp 0.4-0.6 x 0.7-0.9 mm; sclereid clusters often contain a central idioblast. Cells of innermost mesocarp layer beneath sclereid cluster layer, 10-20 cells thick (0.1-0.16 mm). Endocarp palisade layer 120-156 µm thick. Integument 8-12 cells thick (0.1-0.2 mm), transfusion layer 20-30 µm. Embryo containing idioblasts fills seed cavity.

*Specimens examined:* P1060 E bot, P1213 $D_2$ bot, P1326 $E_2$ bot (Figs. 6.1-6.6):deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

***Description*:**

GENERAL SEQUENCE OF DEVELOPMENT. A sequence of developmental stages was observed from flowers (Figs. 6.1A, 6.1B) to early stages after anthesis (Figs. 6.1C-E, 6.2) to immature fruits (Figs. 6.3, 6.4, 6.5), and to mature fruits (Fig. 6.6), including isolated seeds with adhering inner pericarp remnants. In conjunction with pericarp development, the seed and embryo enlarge also. Receptacle tissue enlarges with the fruit to form a shallow sclerotic cupule at maturity, and tepals persist on the receptacle up to the final stages of maturity. Although epidermis is well preserved, guard cell arrangements were difficult to observe in oblique sections of these globose fruits. Fruits can appear superficially distinct depending on the state of maturation, and several developmental stages are described.

FLOWERS AND EARLY FRUIT DEVELOPMENT. The earliest stages of maturity in the developmental sequence show flowers of *Similkameena borealis* Little et Stockey with stamens and tepals present (Figs. 6.1A, 6.1B). The trimerous, pedicellate flowers bear a single carpel and have an innermost, extrorse androecial whorl, and two outer, introrse androecial whorls (Figs. 6.1A, 6.1B). Two whorls of tepals surround the stamens, and trichomes are present on the tepals and hypanthium, but are absent from the surface of the gynoecium (Fig. 6.1A). The carpel is enlarged, are degraded (Figs. 6.1C-D). A single apical ovule is visible at this stage, and tepals remnants persist (Figs. 6.1C-D, arrowheads). The style is narrow and about the same length as the ovary (Figs. 6.1D, 6.1E).

Some specimens at this early developmental stage have well-preserved ovules inside the carpel (Fig. 6.2). Idioblasts are present in the carpel/fruit wall (FW), and trichomes are present on the receptacle and tepal remnants (Figs. 6.2A, 6.2B). The inner and outer epidermis of the carpel are composed of short cells with rectangular outlines in section view (Fig. 6.2C). Trichomes are unicellular, with simple bases (Fig. 6.2B). A single elongate embryo sac (ES) is present, within the nucellus (N), and two integumentary layers are present (Fig. 6.2C). The inner integument (II) is 2-4 cells thick, and the outer integument (OI) is 5-10 cells thick.

IMMATURE FRUIT STAGE. Later developmental stages bear thicker fruit wall and further enlarged ovulses (Fig. 6.3). Styles are less distinct on the enlarged carpel (Fig. 6.3A). The young pericarp shows some cellular differentiation and vascular strands are more prominent in the inner fruit wall (Figs. 6.3A, 6.3E; IFW), and cells of the inner carpel are often filled with dark contents (Fig. 6.3B). In longitudinal section the innermost cell layer of the fruit wall starts to form a palisade (Pa) of rectangular cells, similar to those of the epidermis (Figs. 6.3A, 6.3B, 6.3D). This innermost layer has cells with somewhat wavy outlines in transverse (Fig. 6.3D) and oblique section (Fig. 6.3B, 6.3D). The mesocarp contains thin-walled cells and idioblasts (Figs. 6.3A-C, 6.3E).

The apical ovule is more enlarged at this stage, and the inner integument, seen at earlier stages, has disappeared (Figs. 6.3B, 6.3C). The integumentary layer that remains (I) is uniform (ca. 10 cells thick), but often appears thicker in oblique planes of section (Figs. 6.3A, 6.3E). Vascular strands occur throughout the integument, and cellular embryo tissue fills the seed cavity (Figs. 6.3A, 6.3E).

Specimens at this stage often show receptacles that are thickened into a cupule (Fig. 6.3C). Sclereid clusters are sometimes present at the base of the carpel and in the cupule (Fig. 6.3C). Tepal remnants and trichomes are still present at this stage of development (Fig. 6.3C, arrowhead).

LATE IMMATURE FRUIT STAGE. Most specimens known from the Princeton Chert locality are found at a late immature fruit stage (Figs. 6.4, 6.5). Fruits have enlarged further, and are ovate to ellipsoid, and may have apical stylar remnants (Figs. 6.4A, 6.4B, 6.5A, 6.5B). When cupules are found attached to fruits at this stage, they are shallow (Figs. 6.4A-B, 6.5E). Cupules show more abundant idioblasts and contain thick walled cells (Figs. 6.4A-B, 6.5E), and usually lack tepal remnants and trichomes (Fig. 6.4A-B). However, some tepal remnants are found in a few specimens (Fig. 6.5E, arrows).

Fruit walls are further differentiated into and inner fruit wall layer (IFW) with dark contents in cell lumens (Figs. 6.4A-B, 6.4E), and vascular strands. Just above this inner layer, the mesocarp now contains sclereid clusters, and there is often a central idioblast in each sclereid cluster (Figs. 6.4A-B, arrows, 6.4C, 6.5D). The epicarp/epidermis is radially elongate compared to that in immature fruits (Figs. 6.4C, 6.4E), and the endocarp palisade layer (Pa) has elongated radially (Figs. 6.4E, 6.5F), with cell outlines now appearing stellate in transverse section (Fig. 6.4D). The endocarp palisade sometimes shows discontinuities (Figs. 6.4A, 6.4E, 6.5C-D arrow, 6.5E), but this is due to degradation prior to preservation, or from incomplete preservation, rather than a developmental feature. Idioblasts are more abundant in the fruit wall (FW) at this stage of development (Figs. 6.4A-C, 6.4E, 6.5D).

The remaining seed integument appears thinner than at earlier stages of maturity due to the enlargement of the fruit, but is still ca. 10 cells thick (Fig. 6.5F). Seed integument appears thicker in oblique sections (Figs. 6.4E, 6.5A, 6.5B). Cells of the integument are filled with dark contents and the innermost layer is radially elongate (Figs. 6.5A, 6.5B, 6.5F), forming the "transfusion layer" sensu Kasapligil (1951; Corner, 1976). However, this transfusion layer is not always clearly observed in oblique sections (Fig.

6.4E). The dark contents in cells of the integument obscure the vascular strands that are present throughout. A narrowing in the endocarp palisade layer, that forms a beak-like extension, is associated with the apical ovule attachment (Figs. 6.5A, 6.5B). The beak-like structure extends towards the edge of the fruit (Figs. 6.5A; 6.5B, arrows) but would appear as a ridge if viewed intact and from above.

MATURE FRUIT STAGE. There are fewer fruit specimens in a fully mature state than those at earlier stages of development. Fully mature fruits are further enlarged (up to 8 mm in diam), globose, and may have a slight apical protrusion, a minor remnant of the style (Fig. 6.6A). Cupules are rarely found attached at this stage of development, but when present, appear shallow as in the previous stage of maturity, described above.

Exocarp/epidermis of the fruit appears similar to that in the previous stage of development, with a slightly radially elongate cell shape in section view (Fig. 6.6C). Fleshy mesocarp forming a relatively thin layer, often incomplete/abraded, surrounds the inner fruit layers (Figs. 6.6A, 6.6C). Tissues of the mesocarp fruit wall (FW) appear similar to those seen in the previous stage of development, and contain thin-walled cells and idioblasts (Figs. 6.6A, 6.6C). The sclereid clusters (Sc), seen in the previous stage of development, are larger in size and now abut one another (Fig. 6.6). Sclereid clusters form a more or less contiguous, thick layer. Cell patterns in sclereid clusters are radiate or stellate, producing a distinctive cell arrangement (Figs. 6.6B, 6.6C). The inner fruit wall (IFW) of the mesocarp also appears similar to that seen in the previous stage of development, containing cells with dark contents and vascular strands (Fig. 6.6). The palisade layer appears similar to that seen in the previous stage.

The seed enlarges with the fruit and integument/seed coat is the same thickness as in the previous stage of development (ca. 5-10 cells thick). Cells of the integument are generally uniform, isodiametric, often with dark contents, and vascular strands occur throughout (Figs. 6.6A, 6.6B arrows). The innermost layer of the integument is composed of a radially elongate transfusion cell layer. Cells of the embryo completely fill the seed, and no endosperm is present (Figs. 6.6A, 6.6B). At this final stage of maturity, idioblasts are observed in the embryo tissue (Fig. 6.4A, 6.6A).

## DISCUSSION

The Princeton Chert fruits have characters consistent with those of extant Lauraceae (Reid and Chandler, 1933; Kasapligil, 1951; Endress, 1972; Corner 1976; Rohwer 1993; Endress and Ingersheim 1997; Heo et al., 1998; Kimoto et al., 2006). The single seeded unicarpellate gynoecium, forms a globose berry with an small apical stylar remnant at maturity, and a shallow cupule formed from receptacle tissue. Fruits have a fleshy outer pericarp that contains idioblasts, with an inner layer of sclereid clusters, and a single palisade layer composing the endocarp. Endocarp cells are angular, stellate in transverse view, and the endocarp palisade layer forms a protuberance at the apex of the fruit at the point of seed attachment. The mature, apical seed retains an outer integument with an innermost transfusion layer of radially elongate cells, and the embryo fills the seed cavity.

The floral and fruit remains of *Similkameena borealis* are preserved at all the various stages of maturity, with fully mature fruits being found least frequently. Throughout its growing season, the avocado, *Persea americana* Mill., is known to abscise vegetative and reproductive organs regularly (Gazit and Degani 2002). A similar self pruning mechanism is consistent with the recovery of abundant reproductive lauraceous remains preserved at the various developmental stages in the Princeton Chert. Such a scenario would allow for the developmental sequence, from flowers to fruits, to be captured. However, the remains may have been preserved at various developmental stages in the same chert blocks by other mechanisms, such as normal seasonal deciduousness.

The framework for comparative studies of Lauraceae fruits and seeds was put forth by Reid and Chandler (1933) for the purposes of better identification of fossils from the London Clay Flora. Their work found a generally uniform morphology and anatomy across the family. These characters include a variable fruit shape, but that is typically ellipsoidal, with a single, apical seed and receptacles that may develop into cupules of various depths (Reid and Chandler 1933). Receptacles may not develop into a cupule and produce fruits that are free on a more or less enlarged pedicel, but can also develop into flat disks, shallow cupules, or into structures that completely enclose the fruit. Reid and Chandler (1933) observed a suite of anatomical features, including fleshy outer pericarp containing idioblasts, sclerenchyma clusters, and a radially elongate palisade endocarp layer with stellate outlines in transverse view. The single seed in these fruits was observed to have an integument, lack endosperm, and contain a large embryo with flat cotyledons. Subsequent studies have corroborated these data for fruit structure across the family (Kasapligil, 1951; Vaughn, 1970; Corner, 1976; Roth, 1977).

Details of fruit development from late flowers to mature fruits are known unambiguously in *Similkameena*, and show the diagnostic lauraceous characters. These features include the formation of the cupule, enlargement of the carpel, an increase in number of idioblast cells in the pericarp, formation of sclereids in the inner pericarp, elongation of the endocarp into a palisade layer, enlargement of the embryo, loss of the inner integument, and differentiation of the outer integument transfusion layer. Extant members of Lauraceae, where studied, also show a similar developmental pattern (Kasapligil, 1951; Kostermans, 1957; Corner, 1976; Roth, 1977). Additionally, the fossils show the establishment of idioblasts in the embryo at mature stages, and that the discontinuity of the endocarp layer, noted in some extant and fossil Lauraceae (Reid and Chandler 1933), is probably not a developmental feature, but a result of degradation prior to preservation.

Development in lauraceous fruits is well-studied in the economically important *Persea* (Vaughn, 1970; Roth, 1977), but has also been studied in a few other taxa (Kasapligil 1951; Corner 1976). Some species have been studied at early stages of gynoecium development and embryology (Endress, 1972; Endress and Ingersheim 1997; Heo et al., 1998; Kimoto et al., 2006). In all investigations, the gynoecium anatomy is similar to that observed in the Princeton Chert fruits, containing an embryo sac in a nucellus, surrounded by two integuments.

Even in isolation the fruits described in this paper could be confidently assigned to Lauraceae based on the anatomy alone. However, it is considered almost impossible to identify even extant Lauraceae in the absence of floral material (Kostermans, 1957; Rohwer, 1993), and isolated fossil fruits should be assigned to taxa with great care (Reid and Chandler, 1933; Mai, 1971; Rohwer, 1993; Pingen et al., 1994). Therefore, the Princeton Chert fruits are distinctive in the fossil record in that they are connected by a developmental series to the complete inflorescences of *Similkameena borealis*, which allows for an unequivocal taxonomic determination.

***Comparison with fossil taxa.*** The large number of extant species, the difficulty identifying species (Kostermans, 1957; Hyland, 1989; Rohwer, 1993; van der Werff and Richter, 1996; van der Werff, 2001), non-monophyletic generic circumscriptions (Li and Christophel, 2000; Rohwer, 2000; Chanderbali et al., 2001; Li et al., 2004; Rohwer and Rudolph, 2005) and the lack of anatomical knowledge across much of the family contributes to the difficulties in identifying fossil fruits of Lauraceae to genera (Kostermans, 1957; Hyland, 1989; Rohwer, 1993). In spite of these difficulties, numerous fruits have been described in the Cretaceous and Paleogene of North America and Europe (Reid & Chandler, 1933; Scott, 1954; Kirchheimer, 1957; Chandler, 1964; Mai, 1971, 1999, 2001; Mai & Walther, 1985; Manchester 1994; Mickle, 1996; Eklund, 2000; Frumin et al., 2004).

The earliest fossil fruits of certain lauraceous affinity occur in the Late Cretaceous of North America. Drinnan et al. (1990), described *Mauldinia mirabilis* based on whole inflorescences and their subsequent fruits. The young fruits of *Mauldinia* have a cellular endosperm, which is similar to fruits in extant *Cassytha* L., but differs from the non-endospermic condition in *Similkameena*.

A probable lauraceous fruit from the Late Cretaceous of North Carolina, *Grexlupus carolinensis* Mickle (1996), has few preserved characters, but does possess a similar shape and idioblast cells as in extant Lauraceae. Furthermore, the fruit of *Grexlupus* has an innermost palisade layer with undulating cell outlines, typical of Lauraceae (Mickle 1996). Interestingly these fruits come from the same locality as three known lauraceous flower types (Eklund 2000), which are all distinct from *Similkameena* (Chapter 5). However, the remains of *Grexlupus* were not ascribed to any floral remains (Eklund 2000), and should be reinvestigated to clarify the diversity of Lauraceae at this fossil locality.

Reid and Chandler (1933) described eight lauraceous fruit types from the Paleogene London Clay Flora. Four fruit types were assigned to four extant genera, *Endiandra* Brown, *Cinnamomum* Scheaff, *Beilschmiedia* Nees, *Litsea* Lamarck; while four new genera were erected to accommodate other fossils *Crowella* Reid and Chandler, *Protoravensara* Reid and Chandler, *Laurocarpum* Reid and Chandler, and *Laurocalyx* Reid and Chandler (Reid and Chandler, 1933; Collinson, 1983). Due to the ambiguities within the family with regard to fruit identification, numerous species were placed in morphogenera that are broadly defined: *Laurocalyx* represents fruits with cupules/receptacles still attached, while *Laurocarpum* represents isolated fruits lacking cupule or receptacle tissue (Reid and Chandler, 1933). These two genera allow for placement within the family Lauraceae, but further identification is impossible (Reid and Chandler, 1933; Collinson, 1983).

Although well described, the London Clay Lauraceae, as well as other fossil fruits of Lauraceae, should be reevaluated in light of rapidly progressing phylogenetic and taxonomic framework for the family (Chandler, 1978; Pingen et al., 1994). For instance, fossil fruits from the London Clay that are placed in *Cinnamomum* Shaeff are described as lacking cupules, whereas, the genus typically shows a well developed cupule (Kostermans, 1957). The fruits of *Similkameena* share some important characters with London Clay Lauraceae. It is not entirely clear, based on the illustrations, if the sclereid clusters in the London Clay fruits are similar to those in *Similkameena*. However, based on the descriptions of the material, it is likely that the layer of sclereid clusters is similar to that in the taxa assigned to *Endiandra* and *Beilschmiedia* (Reid and Chandler 1933). Manchester (1994) interprets the "stellate clusters of cells" (Reid and Chandler 1933) to indicate the arrangement of cells (parenchyma or sclerenchyma) that surround the oil idioblasts. This radiating pattern of cells around idioblasts occurs in fruits of *Similkameena*, with an idioblast often found centrally in sclereid clusters of variable cell number. *Endiandra* and *Beilschmiedia*, from the London Clay, also are described as having a discontinuous endocarp layer, and Reid and Chandler (1933) could not determine if this was an artifact of preservation or a feature of the fruit. In *Similkameena*, the endocarp is continuous, but is discontinuous in some specimens due to breakdown of the wall prior to preservation, and not a developmental feature of the fruits. With the exception of the monotypic genus *Crowella*, none of the London Clay fruits have the shallow cupule observed in *Similkameena,* but *Crowella* differs in having an enlarged perianth enclosing the fruit, while the Princeton fossils lack tepal remnants at maturity. As such, *Similkameena borealis* fruits are distinct from all London Clay Lauraceae.

Fruits of Lauraceae are also known from the Clarno Nut Beds Flora (Scott, 1954). Manchester (1994) studied several specimens anatomically, allowing comparisons to the

Princeton Chert fruits. The fruits, asssigned to *Lindera* Thunb., *Laurocarpum* and *Laurocalyx*, are all distinctive from those of *Similkameena*. *Lindera clarnensis* Manchester, based on an endocarp containing an embryo, shares a globose shape and an apical endocarp protuberance with the Princeton Chert fruits (Manchester 1994). However, the cells of the endocarp appear to be polygonal in contrast to the stellate outlines of endocarp cells in *Similkameena*. *Laurocalyx wheelerae* Manchester has a shallow cupule like that of the Princeton fruits, but differs in its prolate shape, and lack of sclerenchyma throughout the fruit (Manchester, 1994). The remaining species are assigned to the genus *Laurocarpum* and lack the distinctive layer of sclereid clusters seen in *Similkameena*, and either have isolated sclereid clusters, or lack sclereids altogether (Manchester, 1994). Interestingly, some of the anatomical features seen in fruits from the Clarno Nut Beds Flora are similar to the immature anatomy seen in the Princeton Chert material, highlighting the potential complication of developmental variation in fossil fruits being mistaken for interspecific variation.

Numerous lauraceous fossil fruits are known in Europe (Mai 1971, 1999, 2001; Czaja 2003). These fruits represent excellently preserved specimens that range from permineralizations to lignitized/mummified fruits, and many are placed in extant genera based on cupule characters and gross morphology (Mai, 1971; Czaja, 2003). However, identifications based on such characters have been considered questionable due to the large amount of variability in the family and problems inherent with current generic concepts (Kostermans, 1957; Rohwer, 1993; Pingen et al., 1994). The more problematic specimens are placed in the morphogenus *Laurocarpum* (Mai 1971). Although some of the species studied have cupules, most extend at least over the bottom 1/3 of the fruit, and/or have tepal remnants attached. Therefore, without any anatomical information, comparisons between these fossils and fruits of *Similkameena* are essentially impossible.

Pingen et al. (1994) reinvestigated *Homalanthus costatus* Mai, and reassigned it to the genus *Cinnamomum* based on detailed anatomical study. The authors sampled numerous species of extant *Cinnamomum* for anatomical comparison, as well as several species in subfamily Cinnamomeae (Kostermans, 1957). Pingen et al. (1994) found that in *C. costatum*, and in other species of *Cinnamomum* the outlines of the endocarp cells are polygonal in transverse view, in contrast to the stellate-undulate pattern found in the Princeton Chert fruits and in other species of extant Lauraceae (Kasapligil, 1951; Corner, 1976; Roth, 1977; Pingen et al., 1994). Characters of the endocarp, mesocarp and epicarp were found to aid in distinguishing taxa in their samples (Pingen et al. 1994). Their study also supports the idea that fruits of Lauraceae have uniform characters across taxa. However, further detailed comparative studies are needed in order to elucidate diagnostic characters for fruits of Lauraceae. Further, it is obvious from the investigation of the Princeton Chert material that characters seen over the development of the fruits should ideally be taken into account, since we observe features along the developmental sequence that could be confused with taxonomically informative characters if specimens were studied in isolation.

***Comparison with extant genera.*** Given the lack of information on extant fruit anatomy and the little variation observed in the few taxa that have been studied, it is difficult to compare the anatomy of *Similkameena* with living genera. The known characters in fruits of Lauraceae are generally uniform (Reid and Chandler, 1933), although the inner sclereid layer and the apical, beak-like endocarp extension seen in the Princeton specimens have only been observed in *Endiandra* and *Beilschmeidia*, by Reid and Chandler (1933). Additionally, numerous extant taxa of subfamily Cinnamomeae, studied by Pingen et al. (1994) have endocarp cells that are polygonal in transverse view, which contrasts with the stellate-undulate shape of endocarp cells seen in most other taxa (Kasapligil, 1951; Corner, 1976; Roth, 1977). However, cupule morphology and the nature of the tepals on mature fruits have been systematically surveyed for the family and allow comparison (Table 6.1, Table 6.2).

While the tepals in *Similkameena borealis* remain attached during early development, they are absent at the time of fruit maturation. Deciduous tepals are found in the majority of extant genera in the family (Table 6.1). However, the tepals of the Princeton fruits might also fall into the subpersistent category, as they are present for all but the later stages of development. The ambiguity of this qualitative character needs refinement.

Cupule characters have been used as a basis for subfamilial classification (Kostermans, 1957). The use of cupule characteristics could provide an important tool in distinguishing intrafamilial groupings, as this character correlates well with some clades resolved from molecular phylogenetic studies (Rohwer, 2000; Chanderbali et al., 2001; Rohwer and Rudolph, 2005). However, until the polyphyly among genera (Chanderbali et al., 2001) has been accounted for, and is reflected in generic circumscriptions, characters will continue to lack diagnostic utility. Among the 53 extant genera of

Lauraceae, the majority lack cupules, have enlarged pedicels, or have cupules that entirely enclose the fruit (Table 6.2). This contrasts with the shallow cupule of *Similkameena*. Among extant taxa that may show shallow cupules, some genera (e.g., *Aniba* Aubl., *Licaria* Aubl. and *Systemonodaphne* Mez) are described as having a double-rimmed cup due to the retention of staminal remnants (Rohwer, 1993). Cupules of variable shape occur in *Actinodaphne* Nees, *Cinnamomum* Schaef., *Litsea* Lam., *Neolitsea* Merr. and *Ocotea* Aubl., while the shallow condition of *Similkameena* is observed in six genera: *Aiouea* Aubl., *Dodecadenia* Nees, *Endlicheria* Nees, *Sassafras* Presl., *Umbellularia* (Nees) Nutt. and *Chlorocardium* Rohwer. Beyond these features, comparison of fruits in isolation is limited to the scant knowledge of anatomy and development across the family. Interestingly, the inflorescences of *Similkameena* share similarities to several species of *Ocotea*, which can also display a shallow cupule on mature fruits.

The Princeton Chert represents an assemblage of plants preserved *in situ* or parautothochtonously (Cevallos-Ferriz et al., 1991) and as such, yields numerous well-preserved specimens that allow for whole plant reconstructions and developmental studies. Such studies are essential for a complete understanding of the biology and morphology of fossil plants. The value of more complete plant concepts in the fossil record is essential for useful reconstructions of evolutionary history (Rothwell and Serbet, 1994; Rothwell, 1999; Hilton and Bateman, 2006). Different stages of development in *Similkameena* fruits could easily be interpreted as different species in the fossil record if found in isolation. Thus, it is crucial to distinguish developmental patterns from mature anatomy and morphology in other fossil studies. In the absence of more fossils as complete as *Similkameena,* the only way to elucidate these patterns is through the study of fruits of living Lauraceae. However, among extant Lauraceae, few have been studied developmentally or anatomically. Despite the abundance of Lauraceae fruits in the fossil record, few are known anatomically and none are understood developmentally, as in this study. Since the sequence of fruit development connects these fruits to inflorescences, *Similkameena borealis* is among the best understood species of both extant and fossil Lauraceae.

## LITERATURE CITED

ANGIOSPERM PHYLOGENY GROUP. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II *Botanical Journal of the Linnean Society* 41: 399-436.

BAAS, P., AND M. GREGORY. 1985. A survey of oil cells in the dicotyledons with comments on their replacement by and joint occurrence with mucilage cells. *Israel Journal of Botany* 34: 167-186.

BASINGER, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 59: 2379-2410.

BASINGER, J. F., AND G. W. ROTHWELL. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 55: 1984-1990.

BERRY, E. W. 1914. The Upper Cretaceous and Eocene floras of South Carolina and Georgia. *Department of the Interior United States Geological Survey Professional Paper* 84: 1–200.

BONEHAM, R. F. 1968. Palynology of three Tertiary coal basins in south central British Columbia. Ph.D. dissertation, University of Michigan, Ann Arbor, Michigan, USA.

CEVALLOS-FERRIZ, S. R. S., R. A. STOCKEY, AND K. B. PIGG. 1991. The Princeton chert: Evidence for in situ aquatic plants. *Review of Palaeobotany and Palynology* 70: 173-185.

CHANDERBALI, A. S., H. VAN DER WERFF, AND S. S. RENNER. 2001. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104-134.

CHANDLER, M. E. J. 1964. *The Lower Tertiary floras of southern England. IV*. British Museum (Natural History), London, UK.

CHANDLER, M. E. J. 1978. *Supplement to the Lower Tertiary floras of southern England.* Part 5. Tertiary Research Special Paper #4. The Tertiary Research Group, London, UK.

CHANEY, R. W., AND H. L. MASON. 1933. A Pleistocene flora from the asphalt deposits at Carpinteria, California. *Carnegie Institution of Washington Publication* 415: 45–79.

COLLINSON, M. E. 1983. *Fossil plants of the London Clay* Palaeontological Association Field Guides to Fossils No. 1. Oxford University Press, Oxford, UK.

CONWENTZ, H. 1886. *Die Flora des Bernsteins Vol. 2 Die Angiospermen des Bernsteins*. Danzig: Willhelm Engelmann.

CORNER, E. J. H. 1976. *The seeds of the dicotyledons* Vols 1, 2. Cambridge University Press, Cambridge, UK.

CRANE, P.R., E. M. FRIIS, AND K. R. PEDERSEN. 1994. Palaeobotanical evidence on the early radiation of magnoliid angiosperms. *Plant Systematics and Evolution Supplement* 8: 51–72.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York, New York, USA.

CZAJA, A. 2003. Paläokarpologische Untersuchungen von Taphozönosen des Unter- und Mittlemiozäns aus dem Braunkohlentagebau Berzdorf/Oberlausitz (Sachsen). *Palaeontographica Abt. B*. 265: 1-148.

DILCHER D. L. 1963. Cuticular analysis of Eocene leaves of *Ocotea obtusifolia. American Jourbal of Botany* 50: 1-8.

DRINNAN, A. N., P. C. CRANE, E. M. FRIIS, AND K. R. PEDERSEN. 1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. *Botanical Gazatte* 151: 370-384.

EKLUND, H. 1999. Big survivors with small flowers: fossil history and evolution of Laurales and Chloranthaceae. Ph.D. dissertation,Uppsala University, Uppsala, Sweden.

EKLUND, H. 2000. Lauraceous flowers from the Late Cretaceous of North Carolina, U.S.A. *Botanical Journal of the Linnean Society* 132: 397–428.

EKLUND, H., AND J. KVAČEK. 1998. Lauraceous inflorescences and flowers from the Cenomanian of Bohemia (Czech Republic, Central Europe). *International Journal of Plant Sciences* 159: 668–686.

ENDRESS, P. K. 1972. Zur vergleichenden Entwicklungsmorphologie, Embryologie and Systematik bei Laurales. *Botanische Jahrbücher für Systematik und Pflanzengeographie*. 92: 331-428.

ENDRESS, P. K., AND A. IGERSHEIM. 1997. Gynoecium diversity and systematics of the Laurales. *Botanical Journal of the Linnean Society* 125: 93-168.

FRUMIN, S., H. EKLUND, AND E. M. FRIIS. 2004. *Mauldinia hirsuta* sp. nov., a new member of the extinct genus *Mauldinia* (Lauraceae) from the Late Cretaceous (Cenomanian-Turonian) of Kazakhstan. *International Journal of Plant Sciences* 165: 883-895.

GAZIN, C. L. 1953. The Tillodontia: an early Tertiary order of mammals. *Smithsonian Miscellaneous Collections* 121: 1-110.

GAZIT, S. AND C. DEGANI. 2002. *In* A. W. Wiley, B. Schaffer, and B. N. Wolstenholme [eds.], The Avocado, 101-133. CABI Publishing, Wallingford, Oxon, UK.

HEER O. 1856. *Flora Tertiaria Helvetiae, II. Die apetalen Dicotyledonen.* Winterthur: J. Wurster.

HEO, K., H. VAN DER WERFF, AND H. TOBE. 1998. Embryology and relationships of Lauraceae (Laurales). *Botanical Journal of the Linnean Society* 126: 295-322.

HERENDEEN, P. S. 1991. Lauraceous wood from the mid-Cretaceous Potomac Group of eastern North America: *Paraphyllanthoxylon marylandense* sp. nov. *Review of Palaeobotany and Palynology* 69: 277-290.

HERENDEEN, P. S., W. L. CREPET, AND K. C. NIXON. 1994. Fossil flowers of Lauraceae from the Upper Cretaceous of New Jersey. *Plant Systematics and Evolution* 189: 29–40.

HERENDEEN P. S., S. MAGALLÓN-PUEBLA, R. LUPIA, P. R. CRANE, AND J. KOBYLINSKA. 1999. A preliminary conspectus of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, USA. *Annals of the Missouri Botanical Garden* 86: 407–471.

HILLS, L. V., AND H. BAADSGAARD. 1967. Potassium-argon dating of some Lower

Tertiary strata in British Columbia. *Bulletin of Canadian Petroleum Geology* 15: 138-149.

HILTON, H., AND R. M. BATEMAN. 2006. Pteridosperms are the backbone of seed-plant phylogeny. *Journal of the Torrey Botanical Society* 133: 119-168.

HYLAND, B. P. M. 1989. A revision of Lauraceae in Australia (excluding *Cassytha*) *Australian Systematic Botany* 2: 135-367

JOY, K. W., A. J. WILLIS, AND W. S. LACEY. 1956. A rapid cellulose peel technique in palaeobotany. *Annals of Botany n. s.* 20: 635-637.

KASAPLIGIL, B. 1951. Morphological and ontogenetic studies of *Umbellularia californica* Nutt. and *Laurus nobilis* L. *Publications in Botany, University of California* 25: 115-239.

KIMOTO, Y., N. UTAMI, AND H. TOBE. 2006. Embryology of *Eusideroxylon* (Cryptocaryeae, Lauraceae) and character evolution in the family. *Botanical Journal of the Linnean Society* 150:187–201.

KIRCHHEIMER, F. 1957. *Die Laubgewächse der Braunkohlenzeit*. Veb Wilhelm Knapp Verlag, Halle (Saale), Germany.

KOSTERMANS, A. J. G. H. 1957. Lauraceae. *Reinwardtia* 4: 193-256.

KOVACH, W. L., AND D. L. DILCHER 1984. Dispersed cuticles from the Eocene of North America. *Botanical Journal of the Linnean Society* 88: 63-104.

KVAČEK, J. 1992. Lauralean angiosperms in the Cretaceous. *Courier Forschungsinstitut Senckenberg* 147: 345-367.

LI, J., AND D. C. CHRISTOPHEL. 2000. Systematic relationships within the *Listea* complex

(Lauraceae): a cladistic analysis based on morphological and leaf cuticle data. *Australian Systematic Botany* 13: 1-13.

LI, J., D. C. CHRISTOPHEL, J. G. CONRAN, AND H-W. LI. 2004. Phylogenetic relationships within the 'core' Laureae (*Litsea* complex, Lauraceae) inferred from sequences of the chloroplast gene *mat*K and nuclear ribosomal DNA ITS regions. *Plant Systematics and Evolution* 246: 19-34.

MACPHAIL, M. K. 1980. Fossil and modern *Beilschmiedia* (Lauraceae) pollen in New Zealand. *New Zealand Journal of Botany* 18:453-457.

MAI, D. H. 1971. Über fossile Lauraceae und Theaceae in Mitteleuropa. *Feddes Repertorium* 82: 313-341.

MAI, D. H. 1999. Die untermiozänen Floren aus der Spremberger Folge und dem 2. Flözhorizont in der Lausitz, Teil II: Polycarpicae und Apetalae. *Palaeontographica Abt. B* 251:1-70.

MAI, D. H. 2001 Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz, Teil II: Dicotyledonen. *Palaeontographica Abt. B* 257: 35-174.

MAI, D. H., AND H. WALTHER. 1985. Die obereozänen Floren des Weißelster-Beckens und seiner Randgebiete. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* 33: 1–260.

MANCHESTER, S. R. 1994. Fruits and seeds of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58: 1-205.

MICKLE, J. 1996. *Grexlupus carolinensis*, a new probable lauraceous fruit from the Late

Cretaceous of North Carolina. *Journal of the Elisha Mitchell Scientific Society* 112: 1–6.

MULLER J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1–142.

PENNER, B. M. 1996. Lauraceous fruit from the Middle Eocene, Princeton Chert (Allenby Formation), British Columbia, Canada. Undergraduate thesis, University of Manitoba, Winnipeg, Manitoba, Canada (unpublished).

PINGEN, M., D. K. FERGUSON, AND M. E. COLLINSON. 1994. *Homalanthus costatus* Mai: a new Miocene fruit of *Cinnamomum* Schaeffer (Lauraceae). *Palaeontographica Abt. B.* 232: 155-174.

POOLE I., H. G. RICHTER, AND J. E. FRANCIS. 2000. Evidence for Gondwanan origins for *Sassafras* (Lauraceae)?, Late Cretaceous fossil wood of Antarctica. *International Association of Wood Anatomists Journal* 21: 463-475.

REID, E. M., AND M. E. J. CHANDLER. 1933. *The London Clay flora*. British Museum (Natural History), London, UK.

RENNER, S. S. 1998. Phylogenetic affinities of Monimiaceae based on *cp*DNA gene and spacer sequences. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 61–77.

RENNER, S. S. 1999. Circumscription and phylogeny of the Laurales: evidence from molecular and morphological data. *American Journal of Botany* 86: 1301–1315.

RENNER, S. S., AND A. CHANDERBALI. 2000. What is the relationship among Hernandiaceae, Lauraceae, and Monimiaceae, and why is this question so difficult to answer? *International Journal of Plant Sciences* 161 (Supplement): S109-S119.

RENNER, S. S. 2004. Variation in diversity among Laurales, early Cretaceous to Present. *Biologiske Skrifter* 55: 441-458.

ROHWER, J. G. 1993. Lauraceae. *In* K. Kubitzki, J. G. Rohwer, and V. Bittrich [eds.]. The families and genera of vascular plants. Vol. 2. Flowering plants, dicotyledons: Magnoliid, Hamamelid, and Caryophyllid families, 366-391. Springer Verlag, Berlin, Germany.

ROHWER, J. G. 2000. Toward a phylogenetic classification of the Lauraceae: Evidence from *mat*K sequences. *Systematic Botany* 25: 60-71.

ROHWER, J. G. and B. Rudolph 2005. Jumping genera: the phylogenetic positions of *Cassytha*, *Hypodaphnis*, and *Neocinnamomum* (Lauraceae) based on different analyses of *trn*K intron sequences. *Annals of the Missouri Botanical Garden* 92: 153-178.

ROTH, I. 1977. Fruits of Angiosperms. Gebrüder Borntraeger, Berlin, Germany.

ROTHWELL, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review* 65: 188-218.

ROTHWELL, G. W., AND R. SERBET. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladisitc analysis. *Systematic Botany* 19: 443-482.

ROUSE, G. E. AND S. K. SRIVASTAVA. 1970. Detailed morphology, taxonomy and distribution of *Pistillipollenites macgregori*. *Canadian Journal of Botany* 48: 287-292.

RUSSELL, L. S. 1935. A Middle Eocene mammal from British Columbia. *American Journal of Sciences* 29: 54-55.

SCOTT, R. A. 1954. Fossil fruits and seeds from the Eocene Clarno Formation of Oregon. *Palaeontographica Abt. B* 96: 66-97.

STOCKEY, R. A. 1983. *Pinus driftwoodensis* sp. nov. from the early Tertiary of British Columbia. *Botanical Gazette* 144: 148-156.

TAKHTAJAN, A. 1997. Diversity and classification of flowering plants. Columbia University Press, New York, New York, USA.

TAYLOR, D. W. 1988. Eocene floral evidence of Lauraceae: Corroboration of the North American megafossil record. *American Journal of Botany* 75: 948-957.

THORNE, R. F. 2000. The classification and geography of the flowering plants: Dicotyledons of the Class Angiospermae (Subclasses Magnoliidae, Ranunculidae, Caryophyllidae, Dilleniidae, Rosidae, Asteridae, and Lamiidae). *Botanical Review* 66: 441-647.

UPCHURCH, G. R., AND D. L. DILCHER. 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. *Bulletin of United States Geological Survey* 1915: 1-52.

VAUGHAN, J. G. 1970. The structure and utilization of oil seeds. Chapman and Hall Ltd, London, UK.

WATSON, L., AND DALLWITZ, M.J. 1992 onwards. The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: 2nd June 2006. http://delta-intkey.com.

WERFF, H. VAN DER. 2001. An annotated key to the genera of Lauraceae in the Flora Malesiana region. *Blumea* 46:125-140.

WERFF, H. VAN DER, AND H. G. RICHTER. 1996. Toward an improved classification of Lauraceae. *Annals of the Missouri Botanical Garden* 83: 409–418.

WEYLAND, H. 1938. Beiträge zur Kenntnis der rheinischen Tertiärflora. III. Zweite Ergänzungen und Berichtigungen zur Flora der Blätterkohle und des Polierschieffers von Rott im Siebengebirge. *Palaeontographica Abteilungen B. Paläophytologie* 83: 123-171.

WHEELER, E. A., AND S. R. MANCHESTER. 2002. Woods of the Eocene Nut Beds Flora, Clarno Formation, Oregon, USA. *International Association of Wood Anatomists Journal* (Supplement) 3.

WHEELER E, R. A. SCOTT, AND E. S. BARGHOORN. 1977 Fossil dicotyledonous woods from Yellowstone National Park. *Journal of the Arnold Arboretum, Harvard Univeristy* 58: 280-306.

WILSON, M. V. H. 1977. Middle Eocene freshwater fishes from British Columbia. *Royal Ontario Museum, Life Sciences Contributions* 113: 1-61.

WILSON, M. V. H. 1982. A new species of *Amia* from the Middle Eocene of British Columbia. *Palaeontology* 25: 413-424.

**Fig. 6.1** *SIMILKAMEENA BOREALIS*, FLOWERS AND EARLY FRUIT DEVELOPMENT. A. Flower in transverse section showing nine anthers (arrows), two whorls of tepals (arrowhead at tepal), and bracts. Trichomes occur on tepals and bracts (at right). Gynoecium out of plane of section. P1060 E bot #1, X 113. B. Flower in longitudinal section with shallow hypanthium, tepals (arrowhead) and stamens (arrow). Gynoecium at center containing single apical ovule. P1213 $D_2$ Bot #1, X 57. C. Oblique section through late flower, showing degrading stamens and attached tepals (arrowhead). Ovary swellen, containing single apical ovule. P1326 $E_2$ bot #5, X 42. D. Transverse section of late flower/early fruit with attached receptacle, tepals (arrowhead at tepal) and swollen ovary with long style. P1060 D bot #6d, X 44. E. Transverse section of late flower/early fruit with attached receptacle, tepals (arrowhead at tepal) and swollen ovary with long style. Ovary contains developing seed. P1060 G #50, X 40.

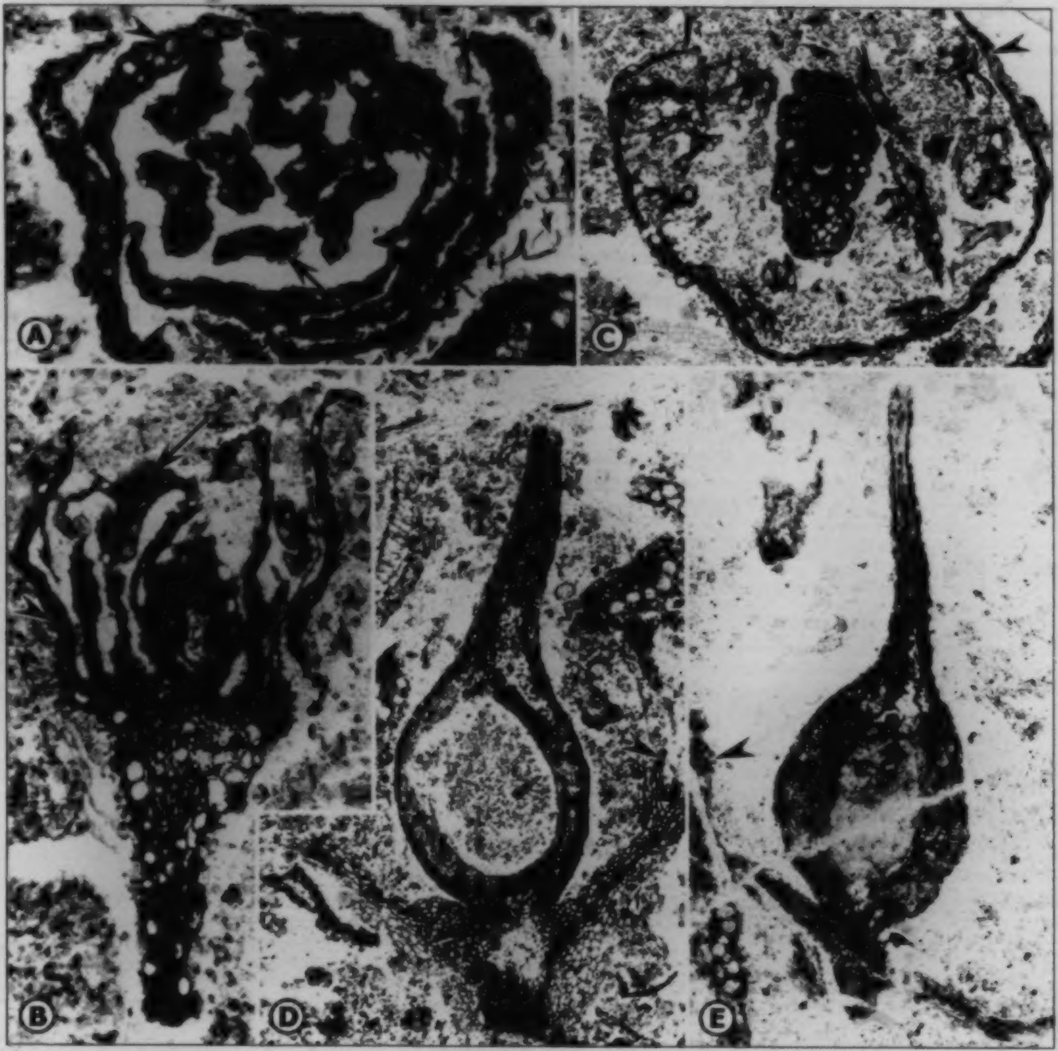
A
C
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**Fig. 6.2** *SIMILKAMEENA BOREALIS*, EARLY FRUIT DEVELOPMENT. Longitudinal section through late flower/early fruit, from same series as in Fig. 6.1E. Style is out of plane of section P1060 G #53. A. Early fruit in longitudinal section containing developing seed. Receptacle and tepals bearing trichomes attached. X 42. B. Enlarged view of unicellular trichomes on tepal. X 249. C. Enlarged view of fruit wall (FW) containing idioblasts. Inner and outer epidermis of pericarp composed of short rectangular cells in section view. Developing seed fills fruit cavity, outer integument (OI) is thicker than inner integument (II), nucellus (N) at center containing linear embryo sac (ES). X 145.

**Fig. 6.2**

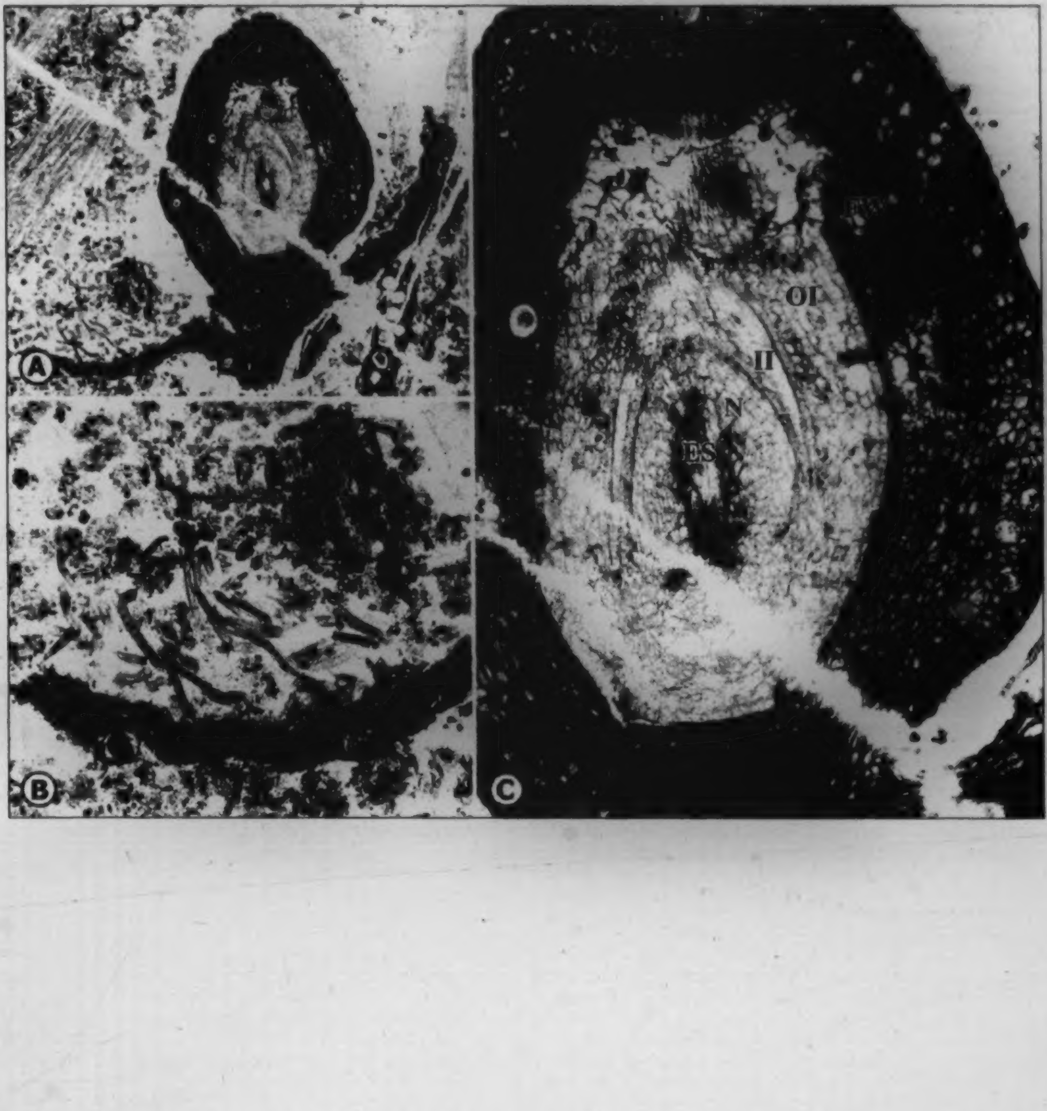

**Fig. 6.3** *SIMILKAMEENA BOREALIS*, IMMATURE FRUIT STAGE. A. Longitudinal section, with early fruit wall (FW), stylar remnant at top, inner fruit wall (IFW), seed with single (outer) integument (I), containing embryo (E). P1095 $D_2$ bot #0, X 35. B. Oblique longitudinal section, tangential view of integument (I), oblique view of inner epidermis/endocarp palisade (Pa). Funiculus at top, dark contents and vascular strands in inner fruit wall (IFW), outer fruit wall (FW) with thin-walled cells. P1288 $B_1$ top #12, X 33. C. Longitudinal section with attached cupule (C), tepal remnants (arrowhead), fruit base contains some sclereids. Integument (I) in tangential view. P1187 B top #20, X 38. D. Inner epidermis/early endocarp palisade layer, same peel series as in B. Thin-walled cells are polygonal to stellate (at center) P1288 $B_1$ top #1, X 68. E. Embryo (E) filling seed cavity, outer integument (I), inner epidermis/endocarp palisade (Pa) adjacent to seed, inner fruit wall (IFW) contains vascular strands, and outer fruit wall (FW) of thin-walled cells and idioblasts. P1095 $D_2$ bot #0, X 71.

Fig. 6.3

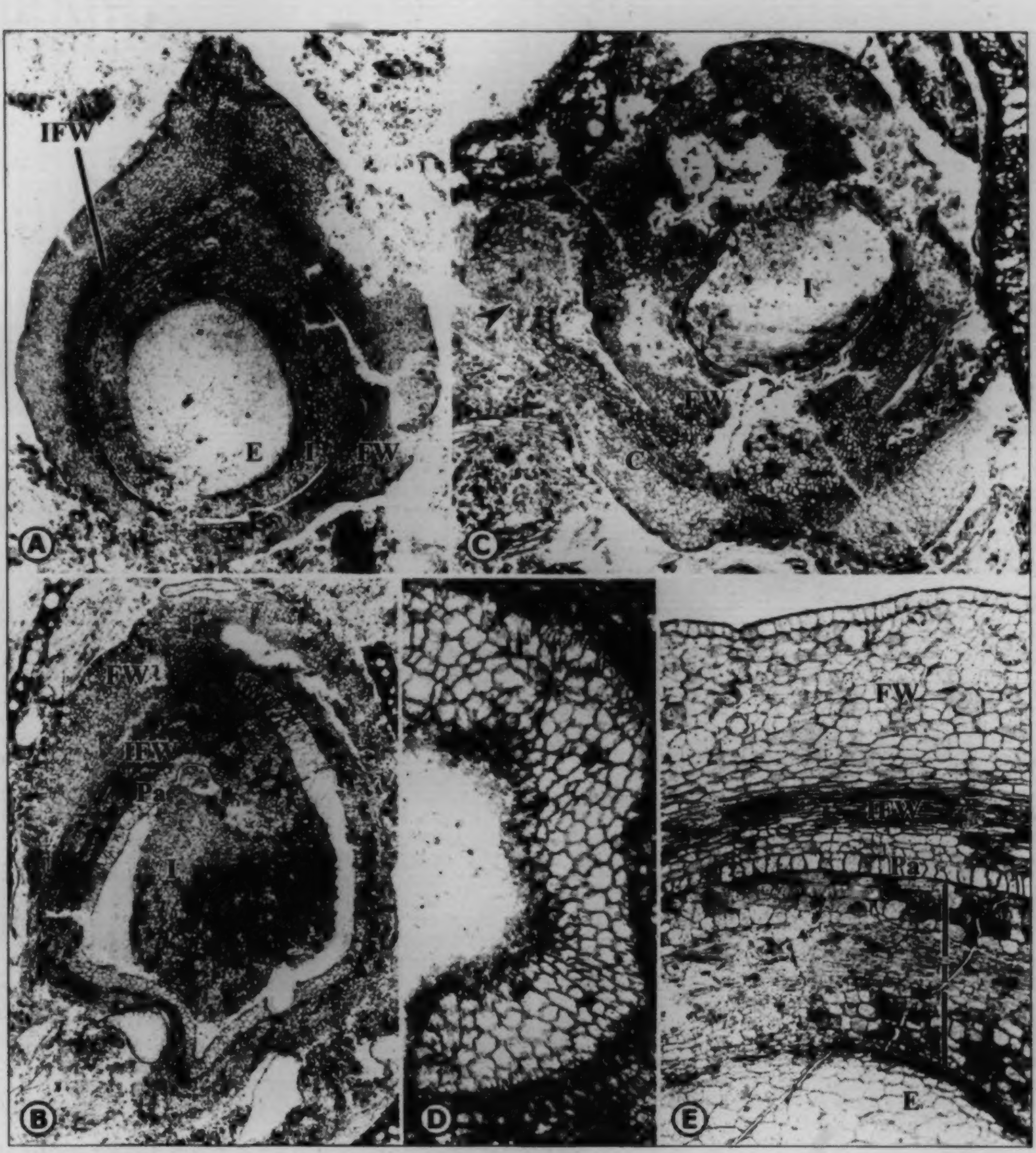

**Fig. 6.4** *SIMILKAMEENA BOREALIS*, LATE IMMATURE FRUIT STAGE. A. Longitudinal section, stylar remnant at top, shallow sclerotic cupule (C) at bottom, outer fruit wall (FW). Sclereid clusters (arrows), inner fruit with dark contents and vascular strands. Radially elongate endocarp palisade (Pa), seed with embryo (E) and integument (I). P1013 $B_3$ top #2a, X 19. B. Oblique longitudinal section, stylar remnant at top, shallow sclerotic cupule at bottom, endocarp palisade and seed at center. Fruit wall with idioblasts, sclereid clusters (arrows). P1013 B bot side3 #0, X 27 C. Fruit wall in tangential section. Radially elongate epidermis at right, scattered idioblasts and sclereid clusters, center and left. P1013C top side2 #31b, X 91. D. Tangential-transverse section of stellate endocarp palisade cells. P1060 D bot #11c, X 97. E. Transverse section with embryo (E) filling seed, outer integument (I), radially elongate endocarp palisade (Pa), inner fruit wall (IFW) with dark contents, outer fruit wall with thin-walled cells, idioblasts, and radially elongate epicarp/epidermis at top. P1326 $F_2$ top #8, X 13

Fig. 6.4

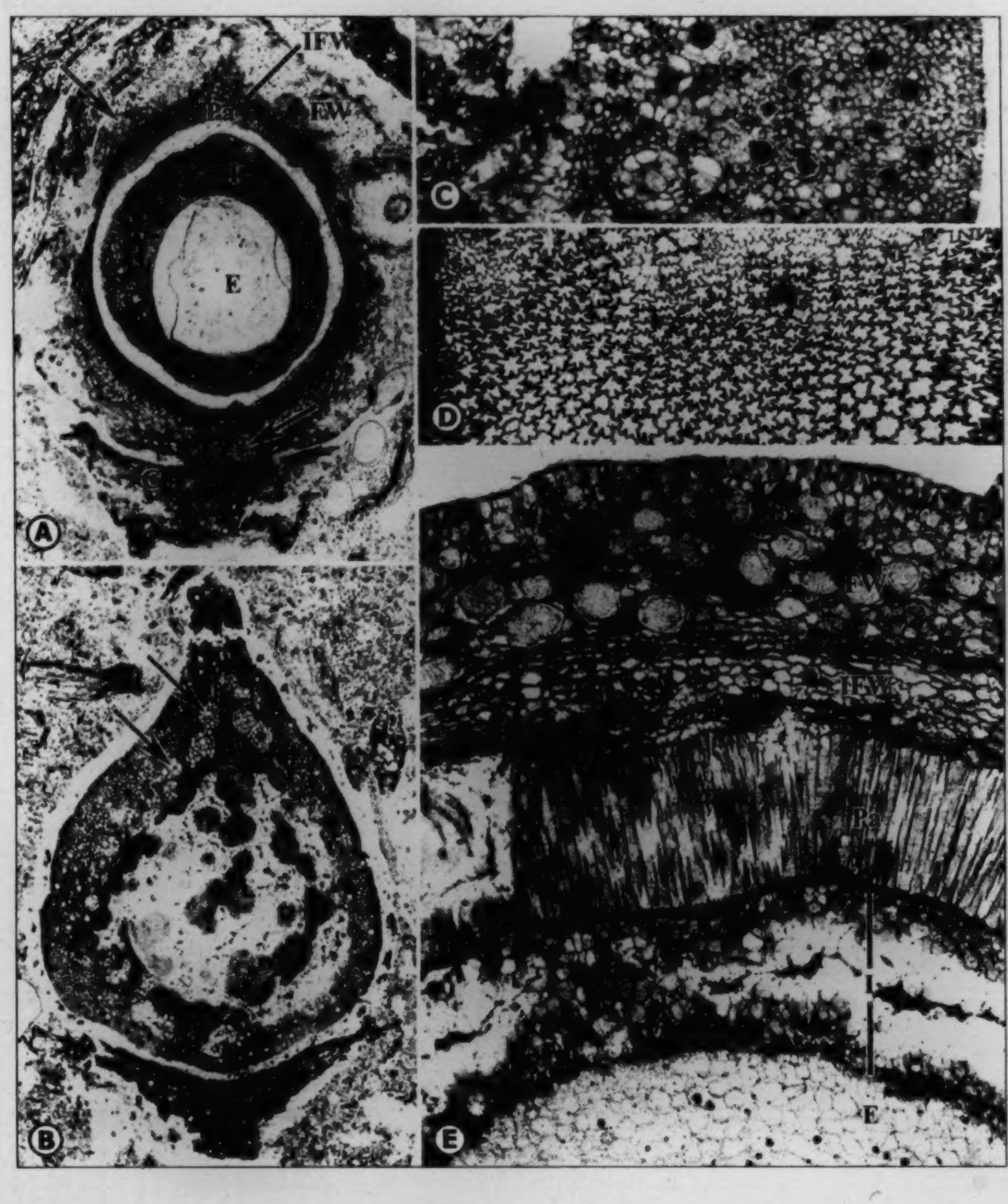

**Fig. 6.5** *SIMILKAMEENA BOREALIS*, LATE IMMATURE FRUIT STAGE CONTINUED. A. Longitudinal section, mesocarp largely missing, integument (I) at bottom, area of attachment at center, endocarp palisade (Pa) thinner near apex, forming beak-like protrusion. Epicarp remnant, at arrow. P1060 D bot #11b, X 40. B. Longitudinal section, same peel series as in A. Integument (I) at bottom, with innermost transfusion layer, funicular area at center, endocarp palisade (Pa) thinner near apex, forming beak-like protrusion. Epicarp remnant at top (arrow). P1060 D bot #6c, X 40. C. Transverse section of inner fruit wall. Integument upper right, endocarp palisade diagonal-center, degraded. P1013 $C_2$ top #12, X 126. D. Whole fruit shown in C, endocarp palisade discontinuity at arrow. P1013 $C_2$ top #12, X 27. E. Longitudinal section of fruit base with cupule containing sclereids, vascular strands, and attached tepal remnants (arrows) P1060 D bot #11c, X 37. F. Transverse section of endocarp palisade (Pa) and adjacent integument (I). Note thin, few-celled integument with innermost, radially elongate, transfusion layer. P1326 $D_1$ top #25, X 137.

Fig. 6.5

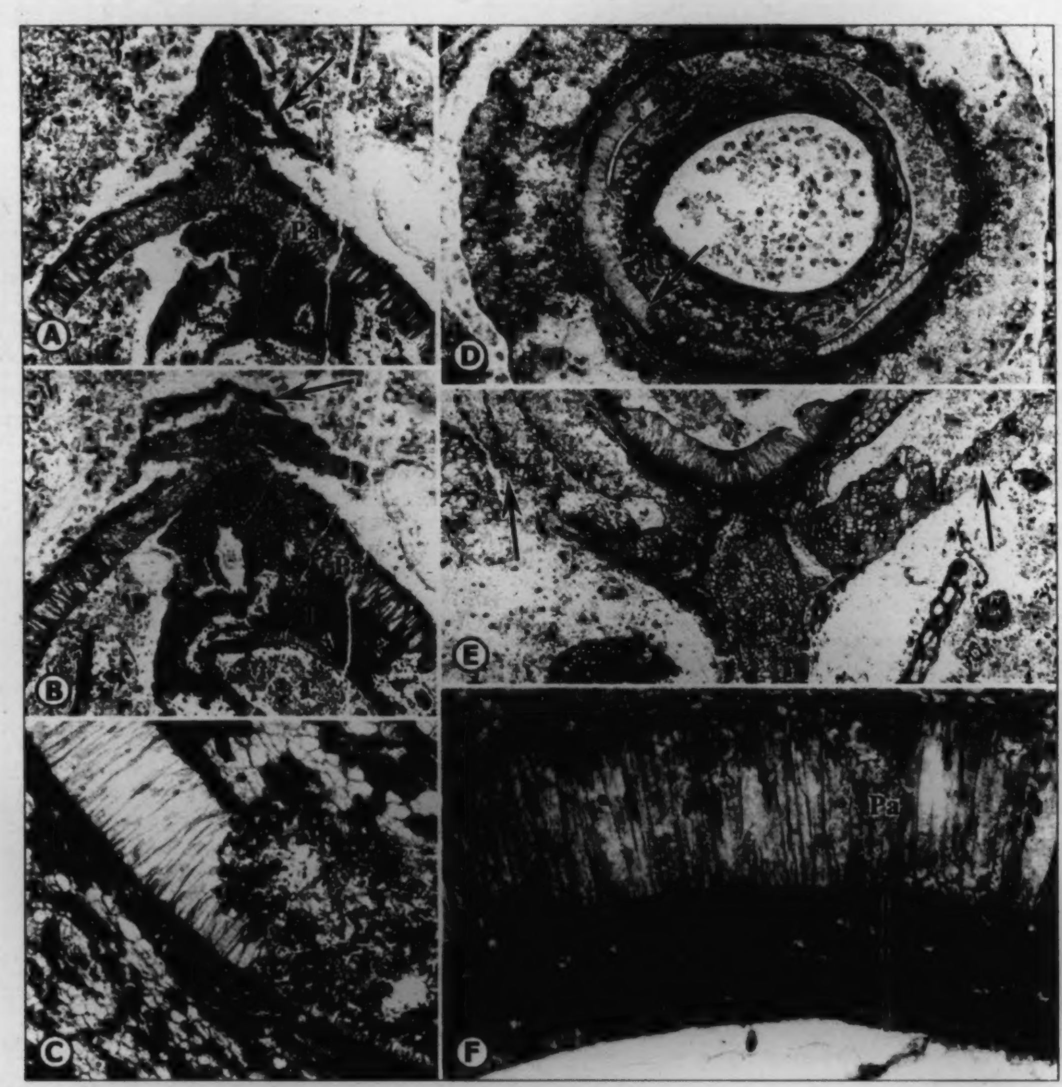

**Fig. 6.6** *SIMILKAMEENA BOREALIS*, MATURE FRUIT STAGE. A. Oblique section of mature fruit with seed and embryo. Note inner sclereid layer, and patchy fleshy outer fruit wall. P1013 $C_2$ top #14, X 15. B. Fruit and seed layers. Embryo (E) at left, filling seed, oblique section of integument (I) containing vascular strands, (note: integument appears thick due to oblique plane of section), endocarp palisade (Pa) is adjacent to seed, and inner fruit wall (IFW) with vascular strands and cells with dark contents. Fleshy fruit wall (FW) with idioblasts contains an inner layer of sclereid clusters in radiate cell arrangements. Sclereid clusters abut. P1013 $C_2$ top #12, X 66. C. Enlarged view of sclereid clusters in radiate cell arrangements. Note proximity of sclereid clusters. P1013 B bot side #2, X 73.

Fig. 6.6

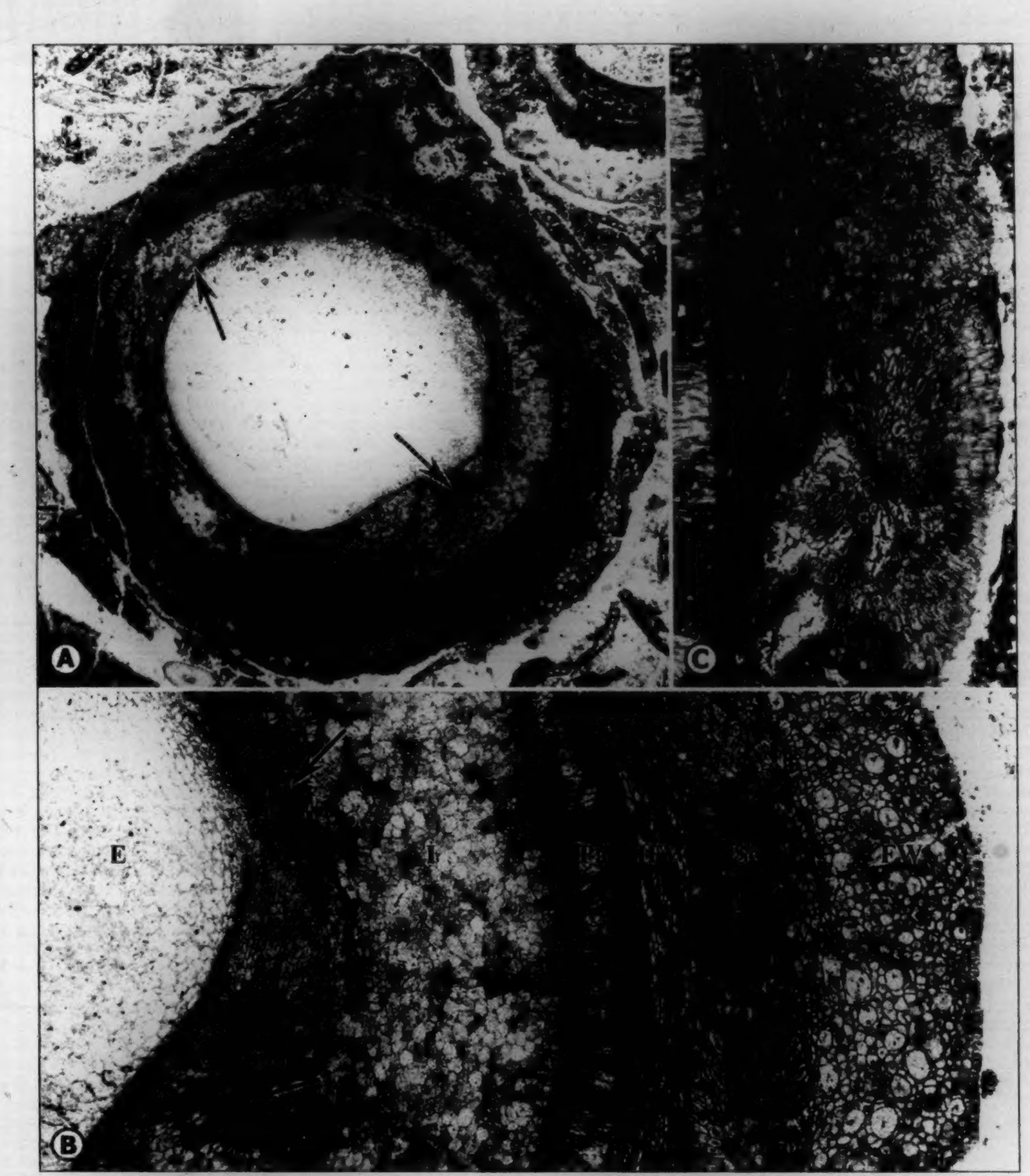

TABLE 6.1. Characters of tepals on mature fruits of extant genera in Lauraceae.

| Tepal character | Genera | | | Notes on genera |
|---|---|---|---|---|
| Deciduous | ***Aniba*** Aubl.<br>***Beilschmiedia*** Nees<br>***Brassiodendron*** C.K. Allen<br>***Cassytha*** L.<br>***Chlorocardium*** Rohwer<br>***Cinnadenia*** Kosterm.<br>***Cryptocarya*** R. Br.<br>***Dodecadenia*** Nees<br>***Endiandra*** R. Br.<br>***Endlicheria*** Nees<br>***Eusideroxylon*** Teijsm. & Binnend. | ***Hypodaphnis*** Stapf.<br>***Iteadaphne*** Blume<br>***Laurus*** L.<br>***Licaria*** Aubl.<br>***Lindera*** Thunb.<br>***Litsea*** Lam.<br>***Mezilaurus*** Kuntze ex Taubert<br>***Nectandra*** Rolander ex Rottb.<br>***Neolitsea*** Merr.<br>***Nothaphoebe*** Blume<br>***Parasassafras*** Long | ***Persea*** Mill.<br>***Pleurothyrium*** Nees ex Lindl.<br>***Potameia*** Thouars<br>***Potoxylon*** Kosterm.<br>***Povedadaphne*** Burger<br>***Rhodostemonodaphne*** Rohwer & Kubitzki<br>***Sassafras*** Presl<br>***Umbellularia*** (Nees) Nutt.<br>***Williamodendron*** Kubitzki & Richter | *Phoebe* and *Apollonias*, base of fruit clasped by indurate tepals |
| Subpersistent | ***Caryodaphnopsis*** Airy-Shaw<br>***Dehaasia*** Blume. | ***Iteadaphne*** Blume<br>***Potameia*** Thouars | ***Urbanodendron*** Mez | |
| Rarely or occasionally persistent | ***Actinodaphne*** Nees<br>***Aiouea*** Aubl. | ***Alseodaphne*** Nees<br>***Ocotea*** Aubl. | | |
| Persistent | ***Apollonias*** Nees<br>***Dahlgrenodendron*** van der Merwe & van Wyk<br>***Hexapora*** J. D. Hook.<br>***Lindera*** Thunb.<br>***Nothaphoebe*** Blume | ***Parasassafras*** Long<br>***Persea*** Mill.<br>***Phoebe*** Nees<br>***Phyllostemonodaphne*** Kosterm. | ***Rhodostemonodaphne*** Rohwer & Kubitzki<br>***Systemonodaphne*** Mez<br>***Umbellularia*** (Nees) Nutt.<br>***Urbanodendron*** Mez | |
| Persistent as minute remnants | ***Anaueria*** Kosterm.<br>***Aspidostemon*** Rohwer & Richter | ***Cassytha*** L.<br>***Cinnamomum*** Schaeff | ***Cryptocarya*** R. Br. | *Cinnamomum*, only basal parts of tepals persist |
| Persistent and enlarged | ***Dicypellium*** Nees & Mart.<br>(***Licaria*** Aubl.) | ***Neocinnamomum*** Liou Ho<br>***Paraia*** Rohwer, Richter & van der Werff | | *Licaria*, only sometimes persistent or enlarged |

Some genera appear more than once due to variation in the genus.

Data from Rohwer (1993), Kostermans (1957), van der Werff (1997).

*Licaria* (= *Gamanthera* van der Werff ), *Cryptocarya* (= *Ravensara* Sonn.)

TABLE 6.2. Cupule characters on mature fruits of extant genera in Lauraceae.

| Fruit/cupule character | Genera | | Notes on Genera |
|---|---|---|---|
| Free on a ± enlarged pedicel | ***Alseodaphne*** Nees<br>***Apollonias*** Nees<br>***Beilschmiedia*** Nees<br>***Caryodaphnopsis*** Airy-Shaw<br>***Dehaasia*** Blume<br>***Endiandra*** R. Br. | ***Hexapora*** J. D. Hook.<br>***Lindera*** Thunb.<br>***Nothaphoebe*** Blume<br>***Ocotea*** Aubl.<br>***Persea*** Mill.<br>***Phoebe*** Nees | *Hexapora* free on accrescent perianth |
| Small discoid cupule on a ± enlarged pedicel | ***Anaueria*** Kosterm.<br>***Brassiodendron*** C. K. Allen<br>***Mezilaurus*** Kuntze ex Taubert<br>***Nectandra*** Rolander ex Rottb. | ***Neolitsea*** Merr.<br>***Potameia*** Thouars<br>***Povedadaphne*** Burger<br>***Williamodendron*** Kubitzki & Richter | *Povedadaphne* on thickened pedicel |
| Minute cupule | ***Cinnadenia*** Kosterm.<br>***Iteadaphne*** Blume<br>***Laurus*** L. | ***Lindera*** Thunb.<br>***Neocinnamomum*** Liou Ho<br>***Parasassafras*** Long | *Laurus*, knob-like on a thickened pedicel; *Iteadaphne*, knob-like |
| Shallow cupule, some with thickened pedicels | ***Aiouea*** Aubl.<br>***Dodecadenia*** Nees<br>***Endlicheria*** Nees | ***Sassafras*** Presl<br>***Umbellularia*** (Nees) Nutt.<br>***Chlorocardium*** Rohwer | *Umbellularia*, lobed cupule |
| Shallow to bowl-shaped double rimmed cup | ***Aniba*** Aubl.<br>***Dicypellium*** Nees & Mart.<br>***Licaria*** Aubl.<br>***Ocotea*** Aubl. | ***Paraia*** Rohwer, Richter & van der Werff<br>***Phyllostemonodaphne*** Kosterm.<br>***Systemonodaphne*** Mez<br>***Urbanodendron*** Mez | |
| Cupule of variable size and/or shape | ***Actinodaphne*** Nees<br>***Cinnamomum*** Schaeff.<br>***Litsea*** Lam. | ***Neolitsea*** Merr.<br>***Ocotea*** Aubl. | |
| Well developed cupule | ***Pleurothyrium*** Nees | ***Rhodostemonodaphne*** Rohwer & Kubitzki ex Lindl. | *Pleurothyrium*, usually lenticellate cupule |
| Deep cupule 1/3 to almost completely enclosed | ***Chlorocardium*** Rohwer<br>***Sextonia*** van der Werff | | |
| Completely enclosed in accressent recepatcular tube | ***Aspidostemon*** Rohwer & Richter<br>***Cassytha*** L.<br>***Cryptocarya*** R. Br. | ***Dahlgrenodendron*** van der Merwe & van Wyk<br>***Eusideroxylon*** Teijsm. & Binnend.<br>***Potoxylon*** Kosterm.<br>***Ravensara*** Sonn. | |
| Completely enclosed in receptacle tissue | ***Hypodaphnis*** Stapf | | |

Some genera appear more than once due to variation in the genus.

Data from Rohwer (1993), Kostermans (1957), van der Werff (1997).

*Licaria* (= *Gamanthera* van der Werff ), *Cryptocarya* (= *Ravensara* Sonn.)

# CHAPTER 7: Conclusions

The purpose of this dissertation was to improve our understanding of whole plants at the well-studied Princeton Chert locality by investigating two plants in detail. Some taxa at Princeton are already known as whole plants, such as *Metasequoia milleri* (Basinger 1976; Basinger and Rothwell 1977; Rothwell and Basinger 1979; Basinger 1981; Basinger 1984), and are the result of detailed investigations on numerous specimens. As previously established in the introduction, it has become clear that a set of reconstruction criteria can be used at the Princeton site. These criteria include: 1) close association of organs in same chert blocks, 2) consistent co-occurrence of organs in a chert layer, 3) anatomical comparisons to extant and fossil taxa, 4) anatomical characters shared by isolated organs 5) developmental sequences that connect isolated organs at different stages of maturity, and 6) attachments of plant organs. Although not always expressed as explicitly as this, these lines of evidence have been crucial tools for testing species concepts of plant remains at the locality.

The chapters of this dissertation utilize these criteria to expand the number of characters for Lythraceae and Lauraceae that occur in the chert. Previous studies on the Princeton Chert (Cevallos-Ferriz et al. 1991; Pigg and Stockey 1996) indicate that the locality promises to provide future lines of research in reconstructing plants, because there are numerous vegetative remains preserved in association with previously described taxa based on fruits or seeds (e.g., *Paleomyrtinaea*: Pigg et al. 1993). Several taxa are also known only from vegetative organs, such as leaves and shoots (Erwin and Stockey 1991), providing an opportunity for future workers to connect these to currently unidentified but associated reproductive remains (Stockey pers. comm.).

CHAPTER 2 - This chapter investigates the vegetative remains associated with fruits and seeds of *Decodon allenbyensis* Cevallo-Ferriz et Stockey. Identification of these woody axes to the genus *Decodon* required a series of criteria including comparative anatomy and attachments of organs. Cellular organization in the aquatic periderm (lacunate phellem) of the fossil axes was compared to that of other Lythraceae, and found to be distinct from *Hiemia* Link et Otto and *Pleurophora* D. Don, but similar to several genera, including *Lythrum* L. and *Decodon* J. F. Gmelin. However, lacunate phellem with similar anatomical organization is also found in numerous unrelated families (Schenk 1889; Sculthorpe 1967). Comparative wood anatomy within order Myrtales was also used to identify the associated fossil axes to the genus *Decodon*. Wood anatomy in the extant *D. verticillatus* (L.) Ell., was also described to supplement the previously described wood anatomy (Baas and Zweypfenning 1979) that the authors considered incomplete due to their study of only one small, immature axis. Further, the root wood anatomy of extant *D. verticillatus* was described here for the first time, including the identification of occasional scalariform perforation plates at growth ring boundaries. Scalariform perforations were previously unknown in the genus (Baas and Zweypfenning 1979; Baas 1986). Although the fossil wood has some characters that differ from the extant species, such as wider vessels and probable tyloses, it was concluded that the fossil wood is that of *Decodon*. The minor differences between stem and root anatomy in the fossil plant were reconciled through the discovery of stems with attached adventitious roots, all with aquatic periderm.

The growth habit of *Decodon allenbyensis* is similar to that of extant *D. verticillatus*, but differs in producing axes that can get much larger than those reported for extant *Decodon*. Thus, my work suggests the need to study extant *D. verticillatus* populations further to determine the upper size ranges of extant plants.

There is strong evidence that the stems and roots, described in chapter 2, are those of the same plant that produced the associated fruits and seeds of *Decodon allenbyensis*. Using the criteria for reconstruction, four lines of evidence support the hypothesized connection of vegetative and reproductive remains of Decodon: 1) fossil vegetative remains are closely associated with the fruits and seeds of *D. allenbyensis*; 2) vegetative axes co-occur among chert layers; 3) fossil axes have almost identical anatomy to the living species *D. verticillatus*; 4) root and stem anatomy of the fossil remains are similar to each other. Based on this partial reconstruction, the Princeton Chert plant represents the only fossil *Decodon* with known internal vegetative anatomy.

CHAPTER 3 – The numerous submerged axes of *Decodon allenbyenis* in the Princeton Chert reveal a series of specimens that illustrates a developmental continuum. Observation of the morphogenesis of the submerged roots was possible through inspection of numerous specimens and peeling through interconnected axes. Early roots, with primary tissues only were connected to older roots, revealing later developmental stages and show the timing of initiation of the different secondary tissues. Many roots have primary aerenchymatous cortex and no secondary vascular tissues while other axes show transitions to secondary xylem and phloem, as well as periderm composed of thin-walled lacunate phellem. The level of detail known for the root development in the fossils exceeds that known for living species in Lythraceae.

Morphogenesis in the fossil roots conforms to what is known for extant *Decodon*. Also, this morphogenesis clearly contrasts with that in aquatic roots of the sister family Onagraceae (Graham et al. 2005) that has similar vegetative anatomy and morphology (Carlquist 1975, 1977). Although both the lythraceous and onagraceous types of morphogenetic patterns contain anatomically similar stages, there are key differences in the origin of some of these, as well as contrasting anatomy at earlier stages in the sequence. Primary cortex aerenchyma in *Ludwigia* (Onagraceae) looks anatomically similar to secondary lacunate phellem that is produced at later growth stages; whereas the primary cortex in roots of *Decodon* form a network of air channels contained in the epidermis and hypodermis. Only a developmental study of the primary and secondary tissues could reveal these anatomical differences.

The rare discovery of mature roots with lacunate phellem attached to a very large woody axis enabled a better understanding of the growth of *Decodon allenbyensis*. This partially compressed, large woody axis (5-15 cm in diam. with 18 growth increments) increases the upper diameter known for the fossil plant. Additionally, these large axes bear a complex type of aquatic periderm. Fossil periderm is in the form of a rhytidome, composed of bands of rectangular phelloid cells without lacunae, alternating with wide bands of non-active, secondary phloem with lacunae and fiber bundles. This complex aquatic rhytidome has not been reported in other living or fossil taxa. It is unclear if this type of rhytidome still exists but is undocumented because there are no reports of extant *Decodon* axes reaching the diameters of the fossil. Thus, the need for further study of extant *Decodon* is demonstrated for this genus, common in the Paleogene of the Northern Hemisphere (Graham et al. 2005).

CHAPTER 4 - The abundant leaves found with *Decodon allenbyensis* have not yet been found attached to stems. However, the abundance of these leaves with other organs of *D. allenbyensis*, as well as their co-occurrence among chert layers, suggested their origin from the same parent plant. To test this hypothesis I surveyed myrtalean leaves, focusing on Lythraceae, in order to compare anatomical characters among the taxa. *Decodon verticillatus* leaf anatomy is described for the first time here. I also illustrate leaf anatomy for the first time for the other extant taxa in the study. Characters found in the fossil leaves are most similar to those of extant Lythraceae (Gin 1909; Keating 1984), in particular, *Duabanga grandiflora* Roxburgh ex DC Walpers. Most important is the diagnostic papillate abaxial epidermis found only in *D. grandiflora* and the fossil leaves.

The results of this study are interesting in that they produce two parallel hypotheses: 1) the leaves were produced by a *Duabanga*-like plant; 2) the fossil leaves were produced by *Decodon allenbyensis*. If the fossil leaves are those of a species of *Duabanga*, it would represent the only known fossil record for this lythraceous genus *Duabanga*, endemic to the rainforests Southeast Asia (Jayaweera 1967). Also, if the leaves represent *Duabanga*, then their presence would support the interpretation that the Princeton locality was warmer than at present (Pigg and Stockey 1996). The near-shore lacustrine environment of the chert (Cevallos-Ferriz et al. 1991) indicates that the leaves of the fossil *Decodon* would have been deposited parautochthonously and preserved along with the other above-ground/above-water organs (Chapter 2). Therefore, the regular, mutual abundance and co-occurrence of the fossil leaves with the other known organs of *Decodon*, is consistent with the interpretation that the fossil *Duabanga*-like leaves were produced by *Decodon allenbyensis*. If the leaves are those of *Decodon allenbyensis*, this species would be distinct from any living Lythraceae in having *Duabanga*-like leaves with *Decodon*-like growth habit, as well as wood, fruit, and seed anatomy. Future discovery the fossil leaves attached to stems is required to test these parallel hypotheses.

CHAPTER 5 - Inflorescences, putatively assigned to Lauraceae (Sun and Stockey 1991), were studied and compared to floral remains in the fossil record, and to the extant genera in the family. Upon investigation, the characters of the inflorescences clearly place these remains in Lauraceae. No complete and mature inflorescence axes have been observed, and the most mature flowers are seen in isolation. Over 75 inflorescences are currently accounted for in the chert. Pedicellate flowers are borne on determinate axes with cymose lateral axes. The main axis and lateral axes terminate in a flower, with proximal units borne oppositely. Each immature inflorescence, lateral axis, and penultimate flower is enclosed by a pubescent bract. The immature flowers are less than 1 mm in diameter, bisexual, actinomorphic, with free stamens and superior ovaries. All terminal flowers, and some penultimate flowers are trimerous with nine stamens in three whorls and lack a fourth whorl of staminodes. Dimerous flowers with four tepals in two whorls, six stamens in three whorls, lacking a staminodal whorl, are found at non-terminal positions of lateral axes.

In all flowers, a pair of glands is found near the base of each filament of the innermost/third androecial whorl. The two outer whorls of stamens are introrse, the innermost whorl is extrose. Receptacles are slightly enlarged with shallow hypanthia, each with a well-developed unicarpellate ovary bearing a single apically attached ovule. Stone cells, oil, and/or mucilage-containing idioblasts are present in all inflorescence axes.

Problematic generic circumscriptions, and overlapping character states within and between genera of Lauraceae make the placement of field collected specimens difficult (Kostermans 1957; Rohwer 1993; van der Werff 2001), and the Princeton material is no exception. However, immature, but complete inflorescences, in bud, provide a relatively large set of characters for comparisons with extant taxa. Therefore, inflorescence and floral characters are compared to extant Lauraceae in a table of morphological characters. Morphological and anatomical characters place the fossils in Lauraceae, but the unique combination of characters requires a new taxon, described here as *Similkameena borealis* gen. et sp. nov. These specimens represent the only anatomically preserved Tertiary floral remains known in North America, the first evidence of dimerous Lauraceae in the fossil record, and the only fossil Lauraceae showing unequivocally a paniculate, cymose infloresence architecture.

CHAPTER 6 - Fruit remains, putatively assigned to Lauraceae (Penner 1996; Little and Stockey 2003), are known from the Middle Eocene Princeton Chert. Inflorescences, previously described in chapter 5 as *Similkameena borealis* gen. et sp. nov. are found in close association with fruits at various stages of development. My investigations have revealed evidence for the connection of the inflorescences to the fruits through a developmental series. The youngest fruits are found with attached floral remnants. Later stages show enlargement of the receptacle, thickening of the fruit wall, and the development of abundant sclereid clusters. Mature fruits are borne on a shallow cup-shaped receptacle, and contain one large seed. Mature fruits have a single endocarp palisade layer made up of radially elongate cells with angular, stellate outlines, an inner mesocarp layer of radiately arranged sclereid clusters, and a fleshy outer mesocarp layer containing numerous idioblasts with golden to dark contents. Mature seeds retain only the outer integument at maturity, and the innermost layer of cells is a radially elongate transfusion layer. Mature seeds are completely filled by cellular embryos containing idioblasts, some with contents.

Fruit characters, described in chapter 6, expand the concept of *Similkameena*, reinforcing the distinct combination of characters of this fossil genus of Lauraceae. This study represents the only developmental study of fossil fruits in the family to date. Fruits appear to be distinct among anatomically studied fossil fruits. However, in isolation, the fruits would not provide a suite of diagnostic characters. Thus, my study highlights the importance of expanded and whole plant concepts for Lauraceae, a family with polyphyletic genera (Rohwer 2000; Chanderbali et al. 2001; Rohwer and Rudolph 2005). Further, the developmental sequence for the fruits of *Similkameena borealis* reveals developmental stages that are comparable to some anatomically known fossil taxa (Reid and Chandler 1933; Manchester 1994). Therefore, it is crucial that a broader sampling of extant Lauraceae be studied anatomically and developmentally to understand the variation in the family. Moreover, previously described fossil fruits (e.g., Mai 1971) should be reexamined anatomically, where possible, to differentiate taxa better and place these fossils in appropriate genera. The sequence of fruit development and connection of these fruits to inflorescences of *Similkameena borealis* results in this species being among the best understood Lauraceae.

CONCLUDING REMARKS - The Princeton Chert represents an assemblage of plants so well preserved that it has been considered a Konservat-Lagerstätten (Stockey 2001). Furthermore, many of the plants are preserved *in situ* or parautochthonously (Cevallos-Ferriz et al., 1991) and as such, the Princeton Chert provides large numbers of well-preserved specimens that allow for developmental studies or whole-plant reconstructions. Contributions to the pool of data on whole plant reconstructions are important since these data are most useful in phylogenetic studies (Hulsenbeck 1991, 1994; Hilton 2004). The use of fossils to construct backbones for phylogenies of organisms is less common, but promises to have utility in reconstructing evolutionary change over time, when compared to studies using extant taxa only (Rothwell and Serbet 1994; Rothwell 1999; Hilton and Bateman 2006; Rothwell and Nixon 2006).

This dissertation expands the concept of *Decodon allenbyensis* which was based originally on fruits and seeds alone, but now includes, vegetative anatomy of stems, roots, leaves, and growth habit. The development of its specialized aquatic tissues are now known and are shown to be unique within Lythraceae. Fruit, seed, wood and periderm anatomy are similar to extant *Decodon*, but the largest fossil axes produce an aquatic rhytidome. This periderm system represents an aquatic bark type that is new to science. The leaf anatomy is most similar to the extant species *Duabanga grandiflora*

(Lythraceae). Thus, all the characters for the plant indicate that *Decodon allenbyensis* is unique among extant Lythraceae in having a mosaic of characters not known among extant taxa, increasing the distinctiveness of this species over the former concept which was based on fruits and seeds alone.

The most recent phylogenetic study in Lythraceae indicates that there are unresolved nodes in the tree (Graham et al. 2005). In particular, the genus *Decodon* appears in various places, depending on the type of analysis. Some trees show *Decodon* as a first diverging lineage in the family, but other trees show *Decodon* to be a basal lineage in a clade that contains *Duabanga* Buchanan-Hamilton, *Lagerstroemia* L., and *Sonneratia* L.f. Unfortunately, the morphological data matrix used (Graham 1993; Graham et al. 2005) does not include many characters that are comparable with the fossils described here. Further, the systematic anatomy for the family is scanty for leaf anatomy and root development which makes the inclusion of the Princeton *Decodon* into such studies difficult. However, subsequent research should endeavor to investigate extant taxa for anatomical and developmental characters because the Princeton Chert plant possesses a unique suite of characters that might result in a more robust phylogeny.

*Similkameena borealis* (Lauraceae) from the Princeton Chert is even more problematic in terms of its future use in evolutionary studies. These difficulties arise from the insufficient knowledge of extant Lauraceae. The current generic concepts are artificial for most larger genera (Chanderbali et al. 2001; Li et al. 2004), and data on anatomy and development is sparse to non-existent, with rare exceptions (Kasapligil 1951). Therefore, it is challenging, at best, to put the well-understood reproductive anatomy and development of *Similkameena borealis* into an evolutionary context. However, it is clear from the studies done here, that *Similkameena* shows a combination of characters that, as a whole, differ from those in all extant genera as well as all known fossil taxa. This distinctness increases with the expansion of the species delimitation originally based on one organ. As with Lythraceae (above), it is imperative that future studies in Lauraceae attempt to improve our knowledge of systematic anatomy and morphology. In Lauraceae, this would have a two-fold benefit: 1) provide new characters for modification of generic circumscriptions, 2) improve the comparison of fossil taxa, and allow for their incorporation into phylogenetic analyses.

By using consistent criteria for reconstructing plants at the Princeton Chert, two plants are now understood at a level of anatomical and development detail that rivals or surpasses many extant taxa in their respective families. The data from these studies sit in a vacuum of knowledge of systematic anatomy that is often barely expanded from the classic studies of Metcalfe and Chalk (1950). The unique combination of characters that fossil plants often possess (Crepet et al. 2004), as well as the accompanying geological data (Hulsenbeck 1994), should be fully utilized, especially in light of studies that show fossil plants to be essential for reconstruction of evolutionary history (e.g., Rothwell and Nixon 2006). As this work progresses, subsequent studies such as those from the Princeton Chert that develop more detailed reconstructions of plants, should be utilized more by workers to produce modified evolutionary hypotheses. In this way, the Princeton Chert, and its biota, promises to be even more noteworthy.

## LITERATURE CITED

BAAS, P. 1986. Wood anatomy of Lythraceae: additional genera (*Capuronia*, *Galpinia*, *Haitia*, *Orias*, and *Pleurophora*). *Annals of the Missouri Botanical Garden* 73:810-819.

BAAS, P., AND R. C. V. J. ZWEYPFENNING. 1979. Wood anatomy of the Lythraceae. *Acta Botanica Neerlandica* 28:117-155.

BASINGER, J. F. 1976. Permineralized plants from the Eocene Allenby Formation of southern British Columbia. Master's thesis, University of Alberta, Edmonton, Alberta, Canada (unpublished).

BASINGER, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 59: 2379-2410.

BASINGER, J. F. 1984. Seed cones of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 62: 281-289.

BASINGER, J. F., AND G. W. ROTHWELL. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 55: 1984-1990.

CARLQUIST, S. 1975. Wood anatomy of Onagraceae: further species: root anatomy: significance of vestured pits and allied structures in dicotyledons. *Annals of the Missouri Botanical Garden* 69: 755–769.

CARLQUIST, S. 1977. Wood anatomy of Onagraceae: additional species and concepts. *Annals of the Missouri Botanical Garden* 64: 627–637.

CEVALLOS-FERRIZ, S. R. S., R. A. STOCKEY, AND K. B. PIGG. 1991. The Princeton chert: evidence for in situ aquatic plants. *Review of Palaeobotany and Palynology* 70: 173-185.

CHANDERBALI, A. S., H. VAN DER WERFF, AND S. S. RENNER. 2001. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104-134.

CREPET, W. L., K. C. NIXON, AND M. A. GANDOLFO. 2004. Fossil evidence and phylogeny: the age of major angiosperm clades based on mesofossil and macrofossil evidence from Cretaceous deposits. *American Journal of Botany* 91: 1666-1682.

ERWIN, D. M., AND R. A. STOCKEY. 1991. Silicified monocotyledons from the Middle Eocene Princeton Chert (Allenby Formation) of British Columbia, Canada. *Review of Palaeobotany and Palynology* 70: 147-162.

GIN, A. 1909. Recherches sur les Lythracées. *Travaux du Laboratoire de Matière Médicale de l'Ecole Superieure de Pharmacie de Paris* 6: 1-168.

GRAHAM, S. A., J. V. CRISCI, AND P. C. HOCH. 1993. Cladistic analysis of the Lythraceae *sensu lato* based on morphological characters. *Botanical Journal of the Linnean Society* 113: 1-33

GRAHAM, S. A., J. HALL, K. SYTSMA, AND S. SHI. 2005. Phylogenetic analysis of Lythraceae based on four gene regions and morphology. *International Journal of Plant Sciences* 166: 995-1017.

HILTON, J. 2004. Relationships among seed ferns as determined from their seeds. Botanical Society of America meeting, Snowbird, Utah, Abstract 208.

HILTON, H., AND R. M. BATEMAN. 2006. Pteridosperms are the backbone of seed-plant phylogeny. *Journal of the Torrey Botanical Society* 133: 119-168.

HULSENBECK, J. P. 1991. When are fossils better than extant taxa in phylogenetic analysis? *Systematic Zoology* 40: 458-469.

HULSENBECK, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* 20: 470-483.

JAYAWEERA, M. A. 1967. The genus *Duabanga*. *Journal of the Arnold Arboretum* 48: 89–100.

KASAPLIGIL, B. 1951. Morphological and ontogenetic studies of *Umbellularia californica* Nutt. and *Laurus nobilis* L. *Publications in Botany, University of California* 25: 115-239.

KEATING, R. C. 1984. Leaf histology and its contribution to relationships in the Myrtales. *Annals of the Missouri Botanical Garden* 71: 801-823.

KOSTERMANS, A. J. G. H. 1957. Lauraceae. *Reinwardtia* 4: 193-256.

LI, J., D. C. CHRISTOPHEL, J. G. CONRAN, AND H-W. LI. 2004. Phylogenetic relationships within the 'core' Laureae (*Litsea* complex, Lauraceae) inferred from sequences of the chloroplast gene *mat*K and nuclear ribosomal DNA ITS regions. *Plant Systematics and Evolution* 246: 19-34.

LITTLE, S. A., AND R. A. STOCKEY. 2003 Permineralized fruits of Lauraceae from the Middle Eocene Princeton chert, British Columbia. Botanical Society of America meeting, Mobile, Alabama, Abstract 225.

MAI, D. H. 1971. Über fossile Lauraceae und Theaceae in Mitteleuropa. *Feddes*

*Repertorium* 82: 313-341.

MANCHESTER, S. R. 1994. Fruits and seeds of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58: 1-205.

METCALFE, C.R., AND L. CHALK. 1950. Anatomy of the Dicotyledons, vol II. Oxford University Press, Oxford, UK.

PENNER, B. M. 1996. Lauraceous fruit from the Middle Eocene, Princeton Chert (Allenby Formation), British Columbia, Canada. Undergraduate thesis, University of Manitoba, Winnipeg, Manitoba, Canada (unpublished).

PIGG, K. P., AND R. A. STOCKEY. 1996. The significance of the Princeton chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. *Washington Geology* 24: 32-36

PIGG, K. B., R. A. STOCKEY, AND S. L. MAXWELL. 1993. *Paleomyrtinaea* a new genus of permineralized myrtaceous fruits and seeds from the Eocene of British Columbia and Paleocene of North Dakota. *Canadian Journal of Botany* 71: 1-9.

REID, E. M., AND M. E. J. CHANDLER. 1933. The London Clay flora. London, England: British Museum (Natural History).

ROHWER, J. G. 1993. Lauraceae. *In* K. Kubitzki, J. G. Rohwer and V. Bittrich [eds.], The families and genera of vascular plants, vol. 2, Flowering plants, dicotyledons: Magnoliid, Hamamelid, and Caryophyllid families, 366–391. Springer Verlag, Berlin, Germany.

ROHWER, J. G. 2000. Toward a phylogenetic classification of the Lauraceae: Evidence from *mat*K sequences. *Systematic Botany* 25: 60-71.

ROHWER, J. G., AND B. RUDOLPH. 2005. Jumping genera: The phylogenetic positions of *Cassytha*, *Hypodaphnis*, and *Neocinnamomum* (Lauraceae) based on different analyses of *trn*K intron sequences. *Annals of the Missouri Botanical Garden* 92: 153-178.

ROTHWELL, G. W., AND J. F. BASINGER. 1979. *Metasequoia milleri* sp. nov., anatomically preserved pollen cones from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 57: 958-970.

ROTHWELL, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review* 65: 188-218.

ROTHWELL, G. W., AND R. SERBET. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Systematic Botany* 19: 443-482.

ROTHWELL, G. W., AND K. C. NIXON. 2006. How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *International Journal of Plant Sciences* 167: 737-749.

SCHENK, H. 1889. Ueber das Aërenchym, ein dem Kork homologes Gewebe bei Sumpfpflanzen. *Jahrbücher für Wissenschaftliche Botanik, Berlin* 20:526–74.

SCULTHORPE, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold, London, UK.

STOCKEY, R. A. 2001. The Princeton Chert. *In* D. E. G. Briggs, and P .R. Crowther [eds.] Palaeobiology II, 359-362. Blackwell Science Ltd, Maledin, Massachusetts, USA.

SUN, Z., AND R. A. STOCKEY. 1991. Lauraceous inflorescences from the Middle Eocene Princeton Chert (Allenby Formation) of British Columbia, Canada. *American*

*Journal of Botany supplement* 78: Abstract 323.

WERFF, H. VAN DER. 2001. An annotated key to the genera of Lauraceae in the Flora Malesiana region. *Blumea* 46:125-140.